DEVELOPMENT OF SOCIAL BEHAVIOUR IN THE RAT

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DEVELOPMENT OF SOCIAL BEHAVIOUR IN THE RAT

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DRUKKERIJ VOS GEMERT

Aan mijn moeder

Aan Christian

Aan Sielke, Jim en ?

DANKBETUIGING

De onderzoekingen waarop dit proefschrift is gebaseerd, werden uitgevoerd in het Psychologisch Laboratorium te Nijmegen, bij de vakgroep Vergelijkende en Fysiologische Psychologie. Veel dank ben ik verschuldigd aan de wetenschappelijke staf van die vakgroep voor de kritische belangstelling en waardevolle aanwijzingen, verkregen gedurende alle fasen van het onderzoek.
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I. DEVELOPMENT OF SOCIAL BEHAVIOUR

I.1. INTRODUCTION

According to Lehrman (1969) the study of animal behaviour may be distinguished by two different types of orientation:

a) the behaviourist orientation, in which the emphasis is on elucidating general laws of behaviour that cut across different species, the particular species chosen for research being merely a technical problem, and
b) the natural-history orientation in which the animal itself and its behaviour are the objects of study.

Sometimes this distinction is falsely regarded as being coincident with the distinction existing between the experimental deductive and the descriptive inductive approaches to the study of behaviour. The behaviourist orientation is perhaps, by confession, merely experimental but the ethological natural-history orientation, on the other hand, is certainly not purely descriptive, both types of scientific approach being employed within it.

Tinbergen (1963) characterizes ethology, the biological study of behaviour, both by its object-observable behaviour together with the biological approach. The biological approach is in turn characterized by the kinds of questions which are asked. The central question: "why do animals behave as they do?", may be regarded in four different ways. Firstly, the "why?" may direct attention to the immediate causation of behaviour: "what made the animal behave as it did now?". Secondly, the question may be construed as: "of what use is the behaviour to the animal?" and the problem is then one of function or survival value. Thirdly, one may ask: "what behavioural changes occur during an animal's development?", a question referring to the ontogeny of behaviour. Lastly, the problem of evolution is involved by asking: "why has this animal adapted to its prevalent environment in this particular way?".

Although overlap may exist, the distinction between causation, function, ontogeny and phylogeny is generally agreed upon. Behavioural development is therefore a major field of study within modern ethology. Ethologists (usually zoologists by training) have repeatedly stressed the importance of a preliminary, exhaustive description of the behaviour of the animals before entering the experimental analytic stage. By preference the animal should therefore be observed

in its natural habitat. Accurate and detailed observation can generate hypotheses which must be subsequently tested both in field and laboratory studies. Such an inductive, observational phase, however tedious it may be, tends to direct attention to relevant questions worth being answered, whilst discarding trivial aspects. As Lehrman (1969) has said: "the enjoyable act of watching the animal do what comes naturally to it in its natural or quasi-natural environment is the starting-point for asking questions that can be transformed into scientific problems.

In the same way, according to ethological principles, the study of behavioural development should start with an observational descriptive account of how behaviour developes in an organism and what changes take place during the course of its lifetime. There is, however, a remarkable lack of such general long-term descriptive studies on the development of behaviour in animal species. A rigid preoccupancy with the nature-nurture dichotomy has led to attention being centered upon specific problems or aspects of behavioural development, such as the effects of early experience or the imprinting phenomenon. However, following severe criticism (Hebb, 1953; Schneirla, 1966; Hinde, 1970) of the nature-nurture distinction which was advanced by classical ethologists such as Tinbergen (1951), studies concentrated more and more on the processes of development upon which the influences of maturation and experience are inseparable (Schneirla, 1966). Some examples of general longitudinal developmental studies are those of Kruyt (1964) on the ontogeny of social behaviour in Burmese red junglefowl, and of Scott and Marston (1950) on the social behaviour development of puppies, together with the study of Williams and Scott (1953) on the development of social behaviour patterns in mice and that of Horwich (1972) on the ontogeny of social behaviour in the grey squirrel.

Despite the overwhelming amount of animal psychology studies in which the rat has been used as the experimental animal, the longitudinal study of behavioural development per se has received minimal attention. The situation is in no way different from that in respect of other species. So far only a very small number of descriptive studies are available. As early as 1899, Small published his investigation on the psychic development of the young white rat. The results of this

qualitative study should be regarded with caution, since observation was based upon a very few individuals, and the young animals had been subjected to a great deal of handling and aversive treatment procedures which may have influenced development. Moreover, only a limited period in the life of the rat was considered, since Small terminated his study when the animals had reached an age of 28 days.
A thorough, qualitative and quantitative approach to the study of rat behaviour development was presented by Bolles and Woods in 1964. However in the quantitative study only a limited number of ill-defined behaviour elements were used. Social behaviour for instance was subdivided into three gross categories: burrow, fight and play, and social grooming. In this case also the lifetime period of observation was limited. Observation was terminated when the animals had reached an age of 36 days. An essentially quantitative study, that covered the behavioural development from birth to maturity (90 days) was performed by Baenninger (1967).
In this study social behaviour development received considerable attention. However the number of patterns distinguished was limited and qualitative description was completely absent. Further disadvantages were the use of a time-sample observation technique, the restriction to male subjects only and the small living spaces in which litters grew up.
A number of descriptive studies bear upon the course of particular display patterns employed by rats. Some examples are the studies of Welker (1964) on the ontogeny of sniffing behaviour and of Blanck et al. (1967) on the ontogeny of orienting behaviour in the rat. Other studies concentrated on ultrasound production by young rats (Noirot, 1968; Allin and Banks, 1971), development of mother-young interaction (Leon and Moltz, 1972) or development of electrophysiological functioning of particular brain areas (Salas et al. 1969). However diverse the approaches employed and the aspects under study may be, they all contribute to unravel the complex phenomenon of behaviour development. What is urgently needed in the study of behaviour of the rat is an accurate and comprehensive description of the development of behaviour in this species, which would enable us to understand and to interpret the results of more analytically oriented studies in this field. The study presented in this thesis is intended to fullfil this need.
We observed the development of the different behaviour patterns in rats by using a qualitative as well as a quantitative approach. As was stated before,

observation of behaviour should preferably take place in the natural habitat of the species, but observation techniques and methods, impose restrictions with respect to the environment in which the behaviour of the animal is to be observed. We endeavoured to solve this dilemma by creating a semi-natural environment that would allow rats to develop and to behave as naturally as possible while at the same time allowing us to make systematic and controlled observations.
It is our hope that the description of behaviour development, resulting from this study, may constitute an adequate frame of reference for more analytically oriented studies, especially in the field of social behaviour development in the rat.

I.2. METHODS

I.2.1. Animals

Four litters, each containing three male and three female rat pups, were observed over a period of 90 days, beginning on the first postnatal day. The animals were the offspring of four female Tryon Maze Dull rats, bred in the Psychological Laboratory of the Catholic University of Nijmegen, the Netherlands. Preliminary studies had convinced us that the choice of this laboratory strain to study behaviour development was a good one. The strain may be seen, to our opinion, as sufficiently representative of the species because of the completeness of the adult behaviour repertoire and the intensity of performance of the various elements observed.

I.2.2. Housing

The litters were housed in large metal cages, measuring 150x75x80 cm. The cages consisted of two equally large compartments, divided by a solid metal wall which could be removed. The cages had a plexiglass front, a wire mesh top and metal sides, back and floor. The floors were covered with sawdust. Water and food were available ad lib. One compartment contained a number of nestboxes placed against the back wall, which were constructed so as to make observations inside the nest possible. The cages were separated by large black cloths, suspended from the

ceiling. Observations of one nest could be made without disturbing the others. Each cage was illuminated by two incandescent lights. A 25 watt red light was kept on permanently. A 100 watt white light was on from 22.00 hours till 10.00 hours, providing a reversed dark-light cycle. The temperature in the air-conditioned room was set at 24°C.

I.2.3. Procedure

A number of pregnant females were placed apart in one compartment of the observation cages several days prior to parturition. At the day of birth, which was counted as day 0, newborn pups were controlled for sex. Each litter, which consisted of at least 3 male and 3 female pups was selected for observation and, if necessary, culled to 3 male and 3 female rats. Observations were started on the first postnatal day for two litters and on the second postnatal day for the other two. During the period 0-30 days litters were observed on alternate days. Litters were housed in one compartment only measuring 75x75x80 cm. during this time. Mothers were removed from the nest during the observation period and placed in the adjacent compartment. At the age of 30 days the pups were weaned and subsequently exposed to the whole observation cage. The pups were weaned at 30 days of age, because it was thought that this age corresponded with the age of weaning under natural conditions. Calhoun (1962) has even observed a mother lactating her 35 day old offspring, but investigations of Leon and Moltz (1971) under controlled laboratory conditions have presented evidence indicating that the lactating period ends by the time young rats have reached an age of 28 days.

In view of the comparatively slow and less abrupt qualitative changes in behavioural development litters were observed once weekly during the period 30-60 days, and only once a fortnight during the period 60-90 days. Litters remained in the observation cages after reaching adulthood (90 days) and non-systematic observations were made thereafter. During the period 0-14 days no distinction was made between individual animals because of technical marking problems as well as for behavioural reasons. At the age of 14 days pups were distinguishably marked using Polycolor Ultrablond Hairdye, thereby making individual recognition of the pups possible on subsequent observation days. The dying technique had to be repeated on the fiftieth postnatal day, during which the cages were also cleaned.

Except for moving the mother from the nest during the recording sessions in the period 0-30 days and for replacing sawdust on the fiftieth postnatal day, the litters were never disturbed.
Observations were made at the beginning of the dark period of the diurnal cycle and were maintained for 15 minutes. Observations were recorded on video tapes.

I.2.4. Behavioural analysis

The behaviour of each individual was continuously scored from videotape re-runs in terms of behaviour categories which had been determined from previous pilot studies. A behavioural element was scored for every second of the observation period, yielding a total of 900 per animal for each observation day. The number of observations carried out during this study gave rise to a total of 453,600.*

I.2.5. Material

Observations were recorded on an IVC 711 videorecorder. Owing to the low lighting levels we used a highly sensitive camera ITC CTC 6000, together with a Canon TV Zoomlens V 6x16. Audible sounds were recorded on videotape, using a Sennheiser M.D. 421 N microphone. A Sennheiser MKH 405 microphone was used for detection of ultrasonic noises. Audible monitoring of these ultrasonic noises was made possible by use of a "rat ultrasonic detector" which effects a translation of the high frequencies down into the human audio band. Listening to these sounds with earphones only occurred during the recording sessions, and no further analysis of the characteristics of the signals was performed.

I.2.6. Behavioural categories

Observation of the behaviour of the animals was carried out according to a previously arranged list of behaviour elements. This list of behavioural patterns or postures was constructed during preliminary observations. Where possible, the nomenclature and definitions of postures or patterns have been copied from Grant and Mackintosh (1963), Barnett (1963), Bolles and Woods (1964), Baenninger (1967) and Timmermans (1977) in order to achieve a standardization of nomenclature in

* Table 1, containing the cumulative record of total times spent on distinct elements per observation day, is printed on pages 70 and 71.

behavioural parameters.

A much more extensive and detailed description of the behaviour of rats may be found in Timmermans (1977). Most of the elements distinguished in the study presented, are derived from that description. However, only the patterns and postures which were observed to occur during the present investigation have been listed. The categorization also corresponds closely with the division as made by Timmermans.

In the method of observation each behaviour element was considered to be a total pattern which was constituted out of distinct components. This method was chosen as we intended to describe general trends in the development of rat behaviour. Each behaviour element was defined as specifically as possible with respect to the aims of the investigation. It did not seem necessary in this stage to use a more detailed and refined list of separate and distinguishable components of elements in describing changes in behaviour during development. Such a method of observation would result in a very extensive list, which would be practically unmanageable. Moreover the analysis of eventually assembled data would produce severe problems.

The list consisted of the following behaviour categories (the numbers in parentheses refer to the pictures in which behaviour patterns and postures of rats are presented).

Social Behaviour

Social contact behaviour

Huddling (Timmermans: pile up)	Animals piling up together in a heap in side the nest, while struggling continually.
Sleep (Timmermans: huddle)	Animals lie quiet while huddling.
Push past	Pushing with the forepaws against siblings.
Crawl across (3)	Animals crawling over siblings, partcularly inside the nest.
Social grooming (17;22)	Licking or chewing the fur of the partner, including aggressive grooming (high-intensity social grooming).
Fall down	Animals fall down onto their side or back as a result of being pushed by a littermate.

Social exploration

Follow	Locomotion directed at a moving partner.
Nosing (13)	Mutual nose to nose contact.
Oral inspection (14)	Sniffing at the mouth region of siblings.
Anogenital inspection (16;18)	Sniffing at the anogenital region of siblings.
Investigate (15)	Sniffing at any part of siblings body except for nose, mouth and anogenital region.

Sexual behaviour

Mount or attempt to mount (20;21)	Palpating the flanks of the partner with forepaws, accompanied by pelvic thrusting.

Intraspecific antagonistic behaviour

Defensive:	
Retreat	Directed movement away from the partner
Keep off (9;18;24)	Trying to keep distance from the partner by pushing with forelimbs and hindlimbs irrespective of posture (sitting, lying down, rearing).
Shrink back	Fast and sudden movement away from the partner with all feet off the ground.
Squirm (23)	Wriggling movements of an animal which lies on its back and is held by a partner.
Flee	Running away from the partner.
Sideways defence (11)	Orientation broadside on to the partner often keeping the partner off with forepaw lifted up or forepaw and hindpaw lifted up and placed against the partner.
Kick (10;22)	Extending one or both hindlimbs violently, directed to the partner

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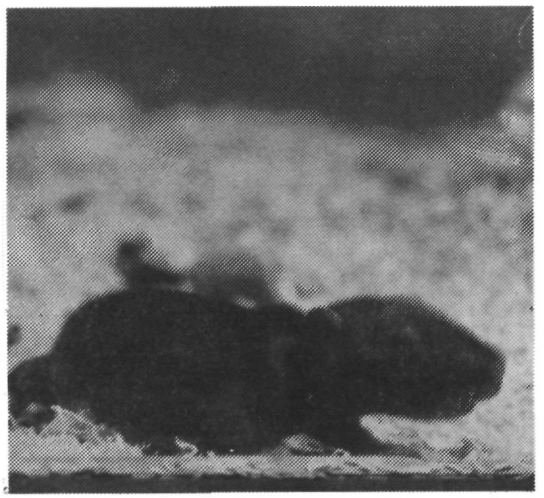

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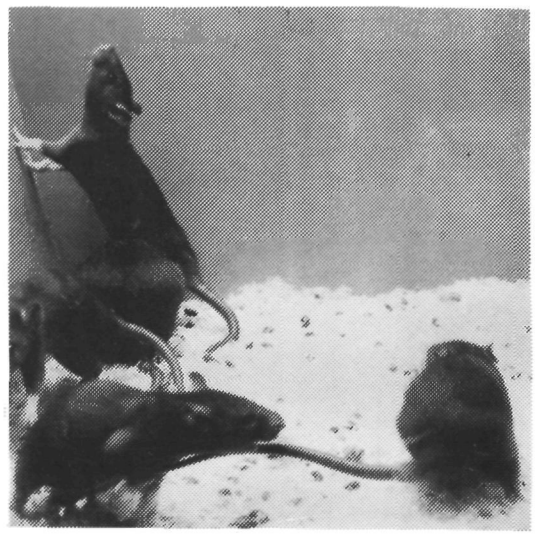

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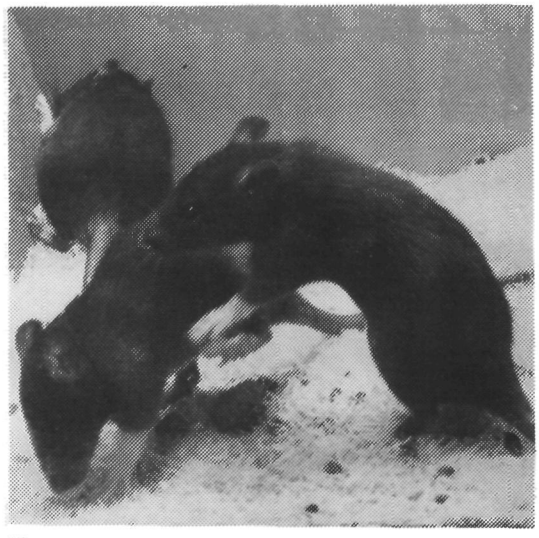

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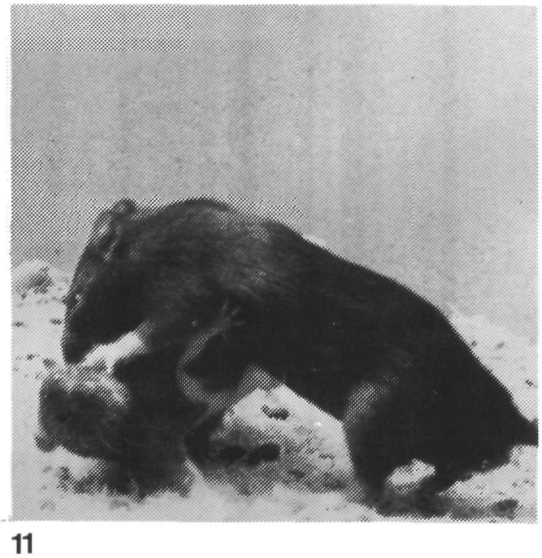

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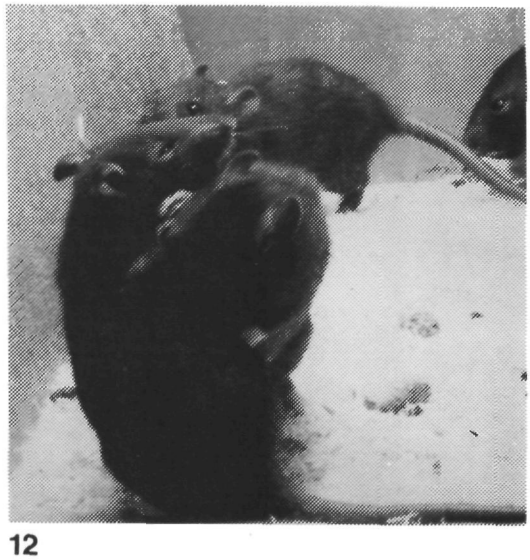

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Offensive:	
Strike	Rapid movement with one or both forepaws onto the partner's face while in a sitting position.
Keep down (23;24)	Orientation at right angle to and over the partner's body while keeping the partner down.
Push over (11)	Pushing a partner over on his side or back.
Fight (12)	Rapid tumbling and jumping in contact with a partner; often accompanied by biting.
Lunge (9)	Jumping movement directed to the partner and bouncing with forepaws against partner's flank.
Pull	Pulling the fur of the partner in the neck or flank, with the mouth.
Drag	Moving a partner over a short distance while tugging at the partner's flank, back or tail with the mouth.
Ambivalent:	
Upright posture (attack or defense)	Offensive or defensive upright position. Two animals holding each other with forepaws, while rearing.
Standing attention	Orientation to the partner while rearing, no contact.
Cling	Holding tight to the partner while both lying down. No movement or only slow movements.
Box	Upright posture with rapid alternating movements of forepaws.

Non Social Behaviour

Locomotion patterns

Crawl (5)	Forward locomotion with forepaws and/or hindpaws, dragging the belly.
Walk (6)	Forward locomotion alternately moving the feet diagonally.

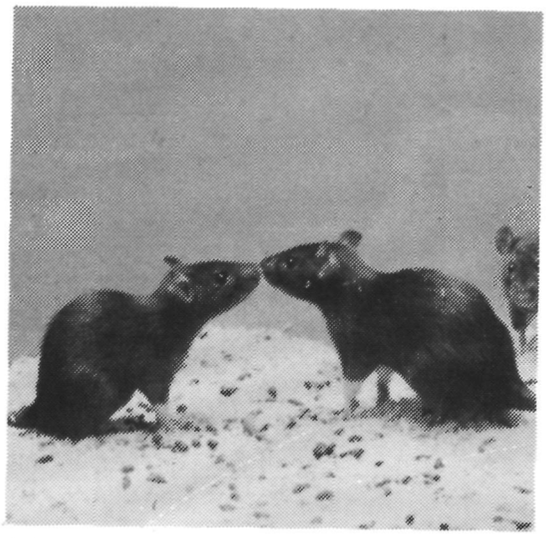
Run	Rapid forward locomotion.
Hop	Rapid forward locomotion with small jumping movements.
Climb	Climbing the nest boxes or wire mesh (including upside down)
Jump	All four feet off the ground.
Turn (8)	Sudden stop and movement in opposite direction, notably in combination with running or dallying.
Dally (7)	Sudden undirected high-intensity movements notably seen in young animals.

Maintenance behaviour (digestion, burrowing and nestbuilding)

Eat	Eating solid foods or faeces.
Drink	Licking the nipple of the water bottle.
Gnaw	Mouthing objects and eventually pulling off pieces.
Pick up	Picking up an object and transporting it.
Grub	Poking the nose into the sawdust with intensively sniffing.
Dig	Pushing the sawdust backwards with forefeet.
Throw up	Pushing the sawdust forward and upward with head and forefeet.

Comfort behaviour

Groom	Chewing and licking the fur.
Scratch (2)	Scratching head and shoulder region with one hindpaw, often combined with intermittently licking and chewing the hindpaw.
Wash (1)	Licking the forepaws and rapid movements with the forepaws alongside the head. Animals in upright sitting posture.
Shake	Quick toss of the head and body to the side in order to remove sawdust or water.



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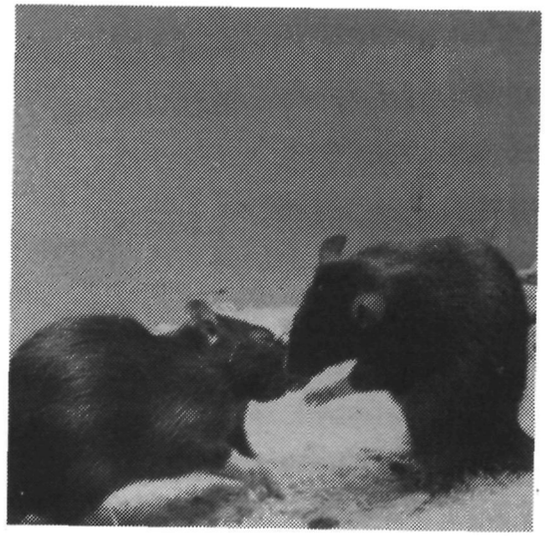

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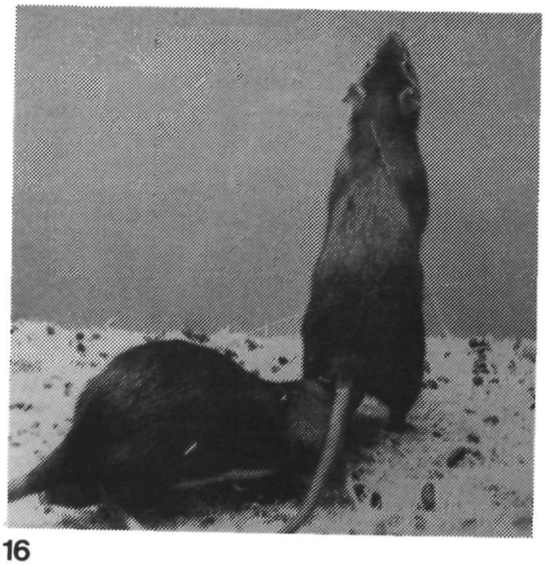

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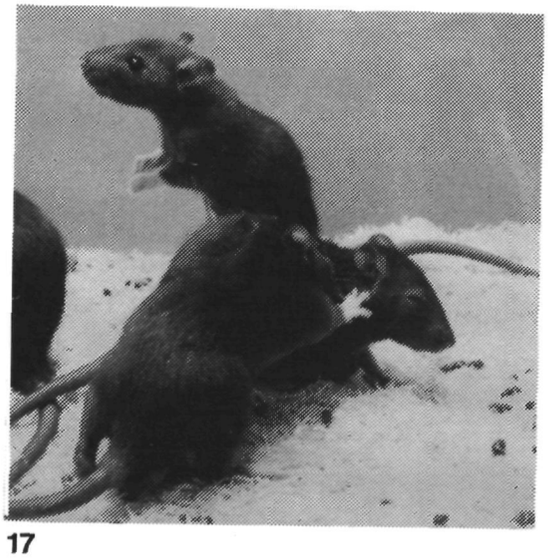

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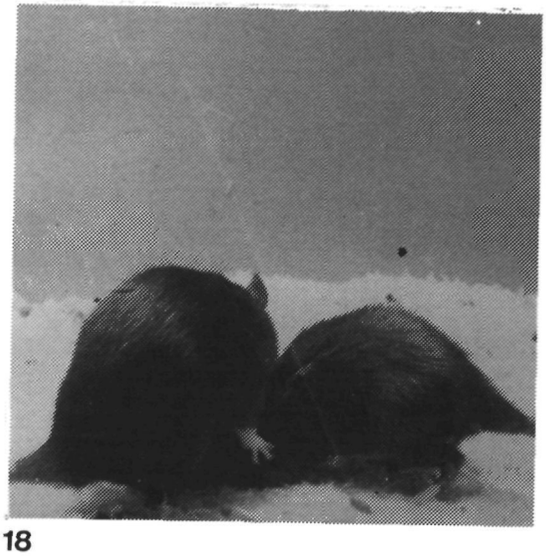

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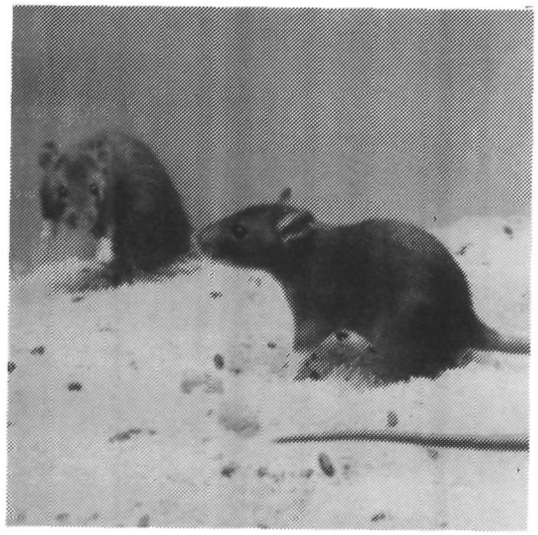

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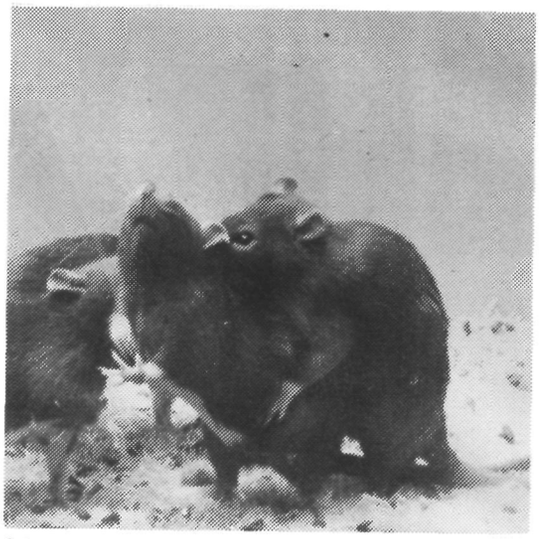

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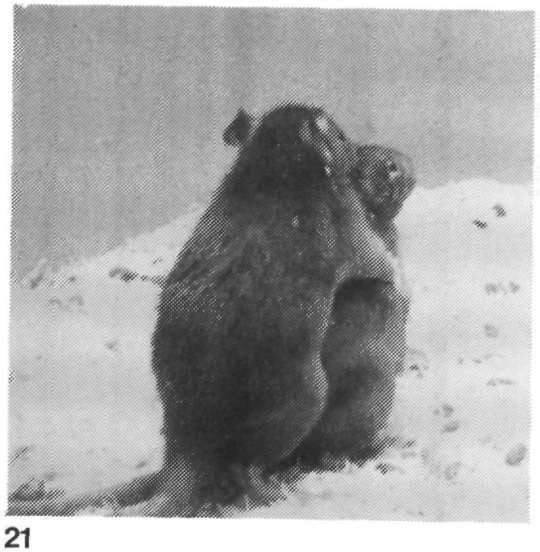

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Yawn	Opening of the mouth to full gape and closing again.
Stretch	Forward extension of the forelimbs and back arched concavely, often combined with yawning.

Other non social activities

Sit (19)	Animal sits quietly on four feet, head and shoulders raised, no sniffing observable.
Rest	Lying alone with eyes closed.
Convulsions	Frantic sudden twitching of head, body and limbs together or separately.
Drink reflex	Pushing the head straight ahead, moving side to side and alternately pushing with the forelimbs back and forth.
Righting response (4)	Twisting of the body, head one way, hindquarters the other, in order to right when in a supine position.
Exploration (6)	Sniffing at objects or in the air irrespective of posture (sitting, lying, rearing).
Paw	Rapid alternating movements with the forelegs while rearing and leaning against an object.

I.3. RESULTS

I.3.1. Neonatal period (0-15 days)

General Information

The newborn rat is an altricial animal. Rat pups are born completely hairless, with a bright red, delicate, almost transparant skin. The first pigment appears on the body surface on approximately the fourth day, and a faint down of hair is observable on the sixth day. The newborn rat has no external eyes, small protuberances only, being visible on the head. Eyes open on about the fifteenth day.

External ears are also absent in the newborn rat. The external auditory meatus opens a few days earlier than the eyes do, on about the twelfth day. The nose is well developed, the newborn pups posses nostrils, though very small. Minute vibrissae are also observable.
The young rats are fully dependent on their mother during the first few days of life. The mother initiates all activities associated with the care of her offspring, initiating nursing bouts, cleaning the nest site and the young and licking the anogenital region of the pups in order to stimulate elimination. With the exception of short eating and drinking periods, the mother is present in the nest site all of the time, invariably crouching over the pups, and thus providing a suitable temperature for the ectothermic young animals.

Social Contact Behaviour

During the period 0-15 days the young animals remained inside the nest for almost the whole of the time. During the observation sessions they spent most of the time piled up in a heap inside the nest (fig. 1).

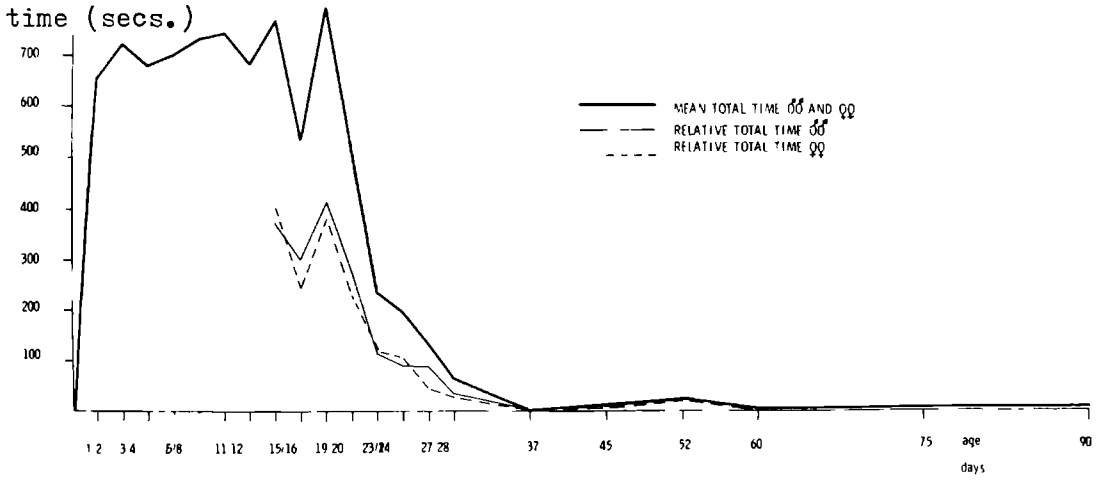


fig. 1. Huddling. Total time spent on huddling at various days of age.

At these times they struggled and wriggled continuously in order to reach the best position which, during the neonatal period, is probably at the bottom of the heap, because of the absence of the mother during the observation sessions.

As stated before, young rats are ectothermic animals. They become gradually less dependent with respect to thermoregulation until gaining full homoiothermia at the age of about 18 days. In this connection it is worth mentioning that our environmental situation was unable to duplicate natural conditions entirely, because of the presence of experimental-observational-devices. The nest had to remain unclosed and nestmaterial was not provided. Furthermore environmental temperature could not be regulated in order to compensate for the absence of the mother from the litter during the period of recording.
Sleep was disturbed every few seconds because of the use of each other's bodies for support, coupled with the presence of frequent twitching of the extremities. This led to an almost permanent reorganization of sleeping positions.

Occasionally vigorous gross twitches, involving the whole body, of one of the pups were observed during sleep, and these have been scored as convulsions (fig. 2).

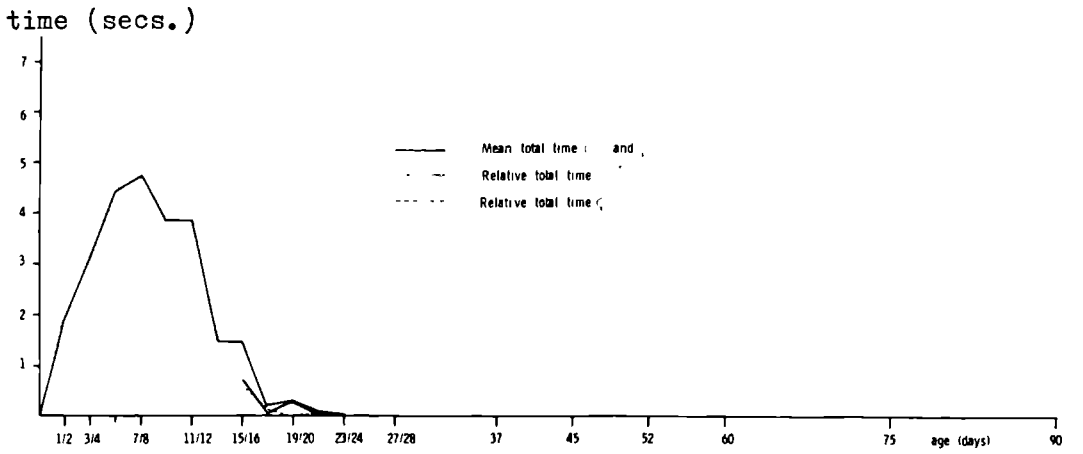


fig. 2. Convulsion. Total time spent on convulsive behaviour at various days of age.

These convulsions reached their peak frequency after the fourth day, which is in accordance with the observations of Bolles and Woods (1964). A rapid decline was observed following the twelfth day.
Rats older than 22 days never exhibited convulsion-like spasms during the observation sessions.
Baenninger (1967) and Gramsbergen (1974) reported an age of 17 days and 20 days respectively, as an end point for convulsions. Differences in methodology and in the rat strain used, may be responsible for these varying results.
Gramsbergen et al. (1970) and Gramsbergen (1974) found that newborn rats spend between 80 and 90% of the total time sleeping. Our results confirm these findings.
Gramsbergen (1970; 1974) draws a distinction between quiet and active sleep, and reports that newborn rats spent most of the time in the behavioural state of qiet sleep. Such a distinction could not be made in this study because of differences in method. Gramsbergen observed individual pups outside the nest while keeping environmental temperature high during observation sessions. We observed individual pups inside the nest and in continuous contact with littermates. The removal of the mother during our observation sessions and the lack of correction for environmental temperature may provide an explanation for our findings.
Whenever the young animals were awake they were seen crawling all over, under and between each other, often pushing with the forepaws against siblings.

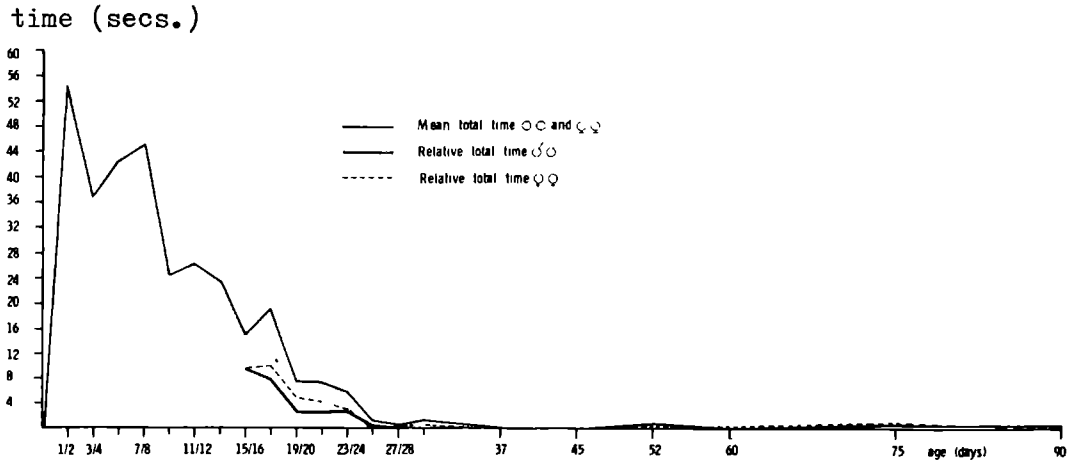


fig. 3. Crawl across. Total time spent on crawling across littermates at various days of age.

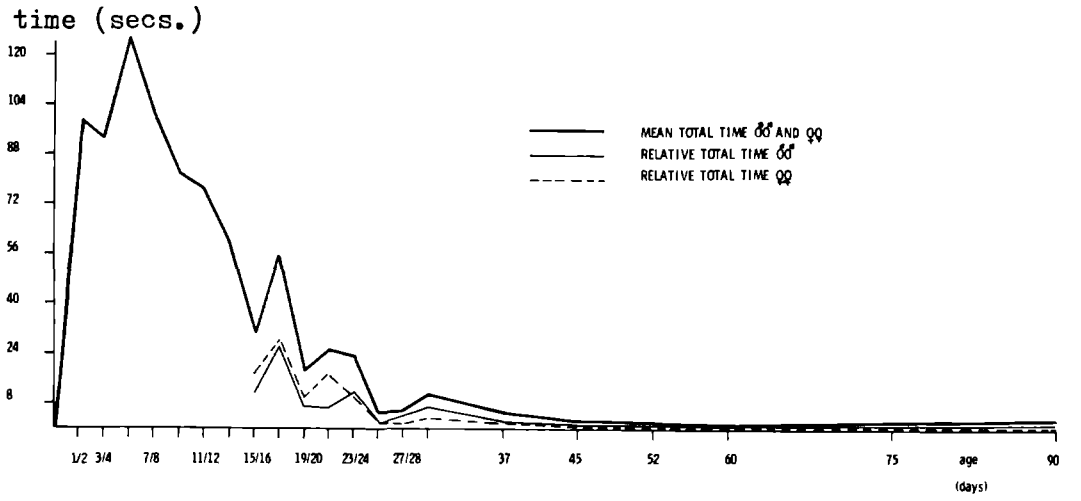


fig. 4. Push past. Total time spent on pushing past at various days of age.

As to crawling across, the behavioural pattern of crawling across could be seen as early as day 1. At that age the young pups used only their forepaws for crawling while dragging the belly and hindlegs along. At about the fourth day they used both forelegs and hindlegs in order to crawl forward over littermates. At later ages when skilled locomotion had been developed, crawl across differs qualitatively from the behaviour scored under the same heading at earlier ages. Juvenile or adult rats simply walked over or climbed over their partners (fig. 3). Pushing against siblings with the forepaws was also observed as early as the first day and this behavioural pattern was performed quite frequently as long as the animals huddled in the nest site and remained continuously in contact (fig. 4). Owing to the frequent crawling and pushing, together with difficulties in maintaning a stable position, young pups often fell down from the heap onto the ground. This occurred most frequently during the first ten days. Following a fall, the animals tried to right themselves by twisting head and body one way and hindquarters the other. This righting behaviour could be observed very frequently during the first two days and declined rapidly thereafter and has never been observed after the fifth day. Beyond that age the animals fell only rarely,

the decline in frequency being probably due to improved skill in maintaining a stable body position.

Animals that fell down and lost contact with the siblings returned to the nest and littermates by crawling. The cues which play a role in guiding this behaviour, are still unknown at the present. Olfactory cues may be involved: the observations of Small (1899) and Welker (1962) indicate that even 1 and 2 day old rats respond to odours with expressive convulsive movements in the case of strong aversive olfactory cues (Small), or with changes in respiration rate and sniffing bouts in the case of mild odours (Welker). Tobach et al. (1967) showed that neonatal rats are capable of discriminating between homecage sawdust and fresh sawdust. Pups also respond with different rates of activity depending upon whether they were placed in their homecage pen or a fresh bare pen.

However, the possibility that reorientation to the nest arises from thermal stimuli from littermates impinging upon heat receptors at the nose, cannot be excluded from our study. Cosnier (1963) pointed out that newborn rats are capable of thermotactic orientation.

Sometimes fallen animals fell asleep (quiet sleep) lying alone without contact with siblings. This behaviour was scored as rest, but it has been observed rather infrequently throughout this study, especially in young animals.

As the animals became older they tended to prefer to sleep alone.

As was mentioned before newborn rats are ectothermic. They are fully dependent on their mothers, crouching over them, for their thermoregulation. Recent investigations (Noirot 1968, 1972; Allin and Banks 1971, 1972; Okon 1971) have stressed the important role played by ultrasound signalling in young rats for eliciting maternal behaviour from the mother rat. Newborn rats are able to produce ultrasonic vocalizations with frequencies between 35 and 55 kHz. According to Noirot (1972) the young rat pup is capable of producing two different kinds of ultrasonic signals in two different situations of discomfort. One signal emitted in response to cold, would elicit retrieval and nest building activities in the mother rat, the other, emitted as a response to uncomfortable tactile stimulation, would inhibit rough handling or licking on the part of the adult. Bell (1974) suggests that this distinction is unlikely, arguing that both vocalizations are produced by an animal in a state of arousal and that both produce a similar state

in nearby animals.

Smotherman et al. (1975) produced evidence in favour of this last hypothesis. Lactating females were unable to retrieve rat pups if ultrasonic calls of neonatal pups only were provided. Olfactory cues were indispensable for eliciting maternal retrieving behaviour in the mother rat. Ultrasonic vocalizations were found to merely elicit searching by the mother rats.

The results of an interesting study by Oswalt and Meier (1975) indicate that thermal cues may be important in eliciting ultrasonic vocalization. Oswalt and Meier also report significant differences in the amount of ultrasonic signalling of neonatal pups lying on bedding soiled with the odour of the mother and that of the littermates and neonatal pups which lay on clean bedding on an empty surface. This is a further indication that young rat pups are able to recognize the home cage odour, and possibly, some inprinting-like process is involved, where olfactory cues serve as the relevant stimuli in providing a bond between mother and young and between siblings. Evidence in support of this hypothesis is provided by the experiments of Marr and Gardner (1965) and Marr and Lilliston (1969). Rats tended to prefer adults smelling of an olfactory substance with which they themselves had been scented early in ontogeny (between 0 and 30 days). Scenting during the first postnatal week appeared to be most effective in establishing the odour preference.

Calhoun (1962) in his extensive study of the ecology of the wild norway rat, reports that he discovered one litter of a mother and seven young rats remaining together, even while continually changing nests, until the young had reached an age of 62 days. A process of olfactory-induced recognition may be responsible for such a bond.

All the authors reporting on ultrasonic signalling, find that this declines with age, and that at the age of $\pm$ 20 days the young conclude signalling altogether. This decline probably reflects the development of homoiothermia in the young rats. In our explorative study we were able to determine the existence of ultrasonic vocalizations, but due to the lack of adequate equipment for analyzing the ultrasonic sounds produced we were unable to provide either qualitative or quantitative results, The neonatal pups used in our study did, however, produce ultrasounds as early as day 1. After the animals had reached the age of 13 days no further

ultrasounds were detected until the 90th day, during which two animals fought vigorously. Pups produced audible squealing sounds almost permanently while huddling inside the nest, probably as a result of more or less painful mutual stimulation or cold. The same squealing sounds are produced by pups struggling to nurse at the nipple of the mother. Whether these sounds (audible and ultrasonic) were components of the same vocalization could not be determined.

Comfort behaviour

Pups were observed making intention movements of face washing and scratching as soon as day 1. Both behaviours were at first performed in a rudimentary, non-functional manner. The face remained untouched while the forepaws made washing movements in the air. Paw licking was also absent during the first 2 days. At day 3 the pups were able to wash the face and they were observed to alternate this with licking the forepaws for a few seconds. Scratching also appears at first in a rudimentary form. The pups move the hindpaws in the air while orienting the head to the feet without actually contacting. This cleaning behaviour becomes functional as early as day 5, and on about day 9 the scratching sequence is completed by gnawing the hindpaws for a few seconds.
Self grooming could be observed for the first time at day 13. This lasted only very briefly because at this age a grooming animal has great difficulties in maintaining a sitting posture for more than a few seconds. Other comfort behaviour patterns such as stretching, yawning and shaking, were present very early in ontogeny but they were performed rather infrequently throughout the observation sessions. Stretching was almost always accompanied by yawning.

Locomotion

Even in the first days of life, neonatal pups were to be seen crawling when they had lost contact. At first they used only their forepaws in forward progression. On the third day, however, they used both forelegs and hindlegs while dragging the belly along (fig. 3). On the sixth day, while crawling, they were able to

hold the head lifted up for a while, and by day 9 they were able to extend the legs more and more. On the eleventh day the first pups were seen walking with the belly off the ground, though walking remains very unstable at this age. At the conclusion of the neonatal period all animals were able to walk. When first walking, the pups stay in the neighbourhood of the nest, gradually extending their walking area. The improvement of coordinated walking beyond the age of ten days is synchronous with a rapid decline in crawling progression. The periods of improvement in early overt motor behaviour coincide exactly with periods of rapid increase in cerebellar neurogenesis (vide infra).

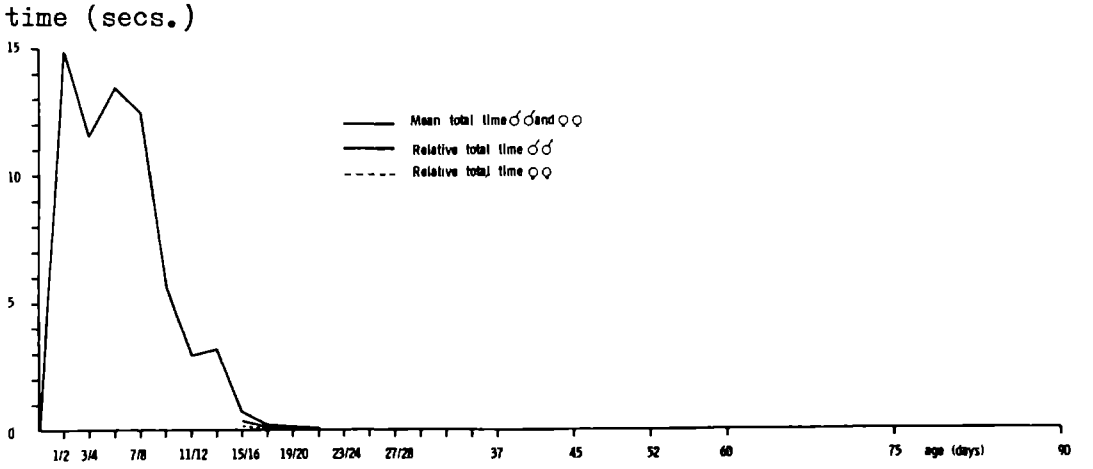


fig. 5. Crawl. Total time spent on crawling at various days of age.

Exploration

All sniffing activities were scored as exploration irrespective of the animal's posture. According to Welker (1964), sniffing behaviour can be divided into four components: polypnea, protraction and retraction of vibrissae, synchronous head movements and fixations, and protraction and retraction of the tip of the nose. During the first days of life polypnea is the only clearly distinguishable component. Gradually, vibrissae and nose and head movements develop until on the nineth day all components are clearly present and observable. A very rapid increase in

sniffing behaviour can be observed from the twelfth day onward.
At the end of the neonatal period the pups began to pick up solid things with the mouth (faecal boluses, pieces of sawdust, food pellets). Whenever this behaviour was observed it was scored as eating because of the morphological similarity with eating behaviour. Pups also occasionally explore the body surface of siblings with the mouth (pulling).

The changes in behavioural development during the neonatal period are very large indeed. From a helpless immature small animal, the rat pup emerges with a behavioural repertoire enabling it to perform, in some respects, quite skillfully, adult-like behaviour.

I.3.2. Transition period (15-21 days)

General information

According to Scott and Marston (1950) and Williams and Scott (1953), the transition period may be defined as a period of changes in physiological capacities both sensory and motor, which precede changes in social behaviour occurring during the following period. The transition period is a relatively short one.

As might be expected, the opening of ears and eyes brings about a dramatic change in the behaviour of the young rats. The ears open just before the beginning of the transition period, and the rats are able to respond to sound stimuli. They orient to mild sounds by lifting the head. Sharp sudden noises cause a typical startle reaction as early as day 13: the animals are observed to jump a few millimeters vertically in the air (Anderson and Patrick 1934; Bolles and Woods 1964).In the transition period vertical jumping sometimes occurs spontaneously. As soon as one animal in a litter began performing this behaviour, it usually spread to the whole litter (personal observation). Occasionally vertical jumping was followed by frantic running around or dallying through the cage.
The opening of the eyes takes place at the beginning of the transition period, occurring at about the 15th postnatal day. It is beleived that the eyes are

immediately functional after opening, since the animals are already able to react to light-stimuli before the opening and, furthermore, adult bioelectrical activity patterns can be obtained from the visual cortex as early as the twelfth postnatal day (Salas et al. 1969). Mere observation of the behaviour of the animals in an unrestricted environment is unsufficient to assess whether the young rats are seeing things or not.

The improvement of coordinated walking progression indicates that motor development continues into the transition period. Contingent with this gradual improvement in gaining control, a change occurs in tempo of movements. During this period the young rat is able to run, dally, jump and climb, and furthermore may be observed to develop and gradually improve its skill in maintaining an upright posture, either sitting on its haunches or standing erect on the hindfeet. At the beginning of the period these behaviour patterns are performed in a rather uncoordinated fashion, lasting only a few seconds. At that time rearing is always accompanied by leaning with the forefeet against the wall.

There is, however, a rapid improvement in muscle strength as well as in coordination: at the end of the transition period the rat pups are able to sit on their haunches or stand erect without support for longer periods.

The period is also one of an increased level of activity, sometimes resulting in bouts of hyperactive behaviour, particularly on the postnatal days 17 and 18. Contrary to the findings of Bolles and Woods, the animals used in our study showed a low level of activity at the ages of 15 and 16 days. This result could be due to the rather stressful operation of dye-marking which took place on the preceeding days 14 and 15 respectively.

In the transition period a shift in the nature and initiative lead of mother-young interaction takes place. From about the 14th postnatal day onwards, the young rat pups approach their mother in order to nurse. Synchronous with the shift in initiative of approach is the emission of a "maternal" pheromone by the lactating mother (Leon and Moltz, 1971, 1972). The emission of the pheromone is altogether completed by postnatal day 28. This time corresponds exactly with the age at which the young cease to be attracted by the mother and weaning is complete. The emission of the maternal pheromone is under endocrinal (prolactine) control (Leon and Moltz 1973). The continuing stimulation by developing young rats induces

high levels of prolactine to be released in lactating females during the neonatal period. The prolactine stimulates increased food intake which is first accompanied by weight gain. Later, increased amount of food is processed in the caecum. The increased growth of bacteria results in a microbial synthesis of an olfactory attractant, which is transmitted to the external environment in the highly concentrated caecotrophe defaecation. The young rats exhibit a preference for approaching the attractant. The young are probably marked by this maternal pheromone. As a result, the pups remain in close contact with each other or stay in the vicinity of the nest site before weaning. Leon (1974) hypothesizes that the transition from liquid to solid food shown by the young rats in the transition period, may also be mediated by the emission of the maternal pheromone in the defaecation.
The young animals were indeed observed to eat the maternal anal excreta, which during this period are somewhat liquid.
In other aspects too, the behaviour of the mother undergoes changes which are synchronous with the changing demands of the developing litter. Retrieving and nest building ceased to be performed. Moreover the mother was observed to sleep or rest alone for a gradually increasing amount of time. In the socialization period the mother was occasionally observed to actively avoid contact with her young, notably during the frequently occurring frantic "playful" activities between the pups.

Social behaviour

During the transition period a limited number of social behaviour patterns and postures were observed for the first time. At the postnatal days 15 and 16 the pups still spent most of their time inside the nest and huddling remained the predominant activity. The animals no longer piled up in a heap, but more often lay down side by side, probably as a result of increasing homoiothermia.
On days 15 and 16 the decrease in activity inside the nest resulted in less mutual pushing and crawling over each other. Very infrequently an animal would leave the nest, one animal was even observed to climb the nest compartments.
On days 17 and 18 more animals left their nests for a short while. They seemed to have an active interest in everything in the environment, exploring the shavings, the next boxes, faecal boluses as well as their littermates. Investi-

gation of the littermates, first observed at the onset of the transition period, increased sharply on days 17 and 18. Grooming of the partner showed the same pattern of development. Grooming at this age consists of gently nibbling the littermates' fur. From walking, exploration and digging, sudden short bursts of hyperactive behaviour emerged, including fragments of social patterns too. The activities were performed with great vigour and lasted only a few seconds or less. Sporadic bursts of frantic dallying or dashing movement alternated with brief digging, grooming and climbing activities. For the first time behaviour elements belonging to the antagonistic repertoire (fighting, dominating, keeping off) were observed. Often only snatches of fighting or dominating behaviour appeared.Once again these behaviour activities, which were performed very jerkily and often incompletely, did usually not last for more than a few seconds. Other social behaviour elements that were noticed for the first time were following and retreating, and these were also performed with great vigour. The animals used a kind of accelerated hopping gait in following or retreating. Occasionally an animal stood erect opposite a littermate without making contact. Striking was also observed for the first time in this period, and occurred without exception in those animals who, having climbed the nest boxes,made striking movements in the direction of littermates trying to do the same. This activity seemed therefore strictly place-dependent. The animals seemed almost to change their activities at random. An animal might successively walk, dally, fight, groom, dig, follow and explore all within a few seconds. The unpredictable character of the often fragmentary and incomplete behaviour activities constituted a serious handicap in making correct observations.

It is our impression that the antagonistic activities observed in social encounters during the transition period are an artefact of the hyperactive locomotor activity combined with the increased interest in anything in the environment that the animals displayed. The young pups almost literally rushed into their littermates, resulting in sporadic bouts of fighting and wrestling behaviour.

It should be noted that Small (1899) and Bolles and Woods (1964) report that young rats do not show any sign of fear at this age and almost instantaneously approach the observer entering the room. Bolles and Woods observed that rats exhibited freezing behaviour for the first time in response to the observer entering the observation area at postnatal day 26. Small (1899) and Welker (1963) observed

freezing in their pups as early as day 18 as a reaction to sudden unusual noises. This discrepancy may be due to a different eliciting stimulus in each case. An animal in the transition period might be hyperreactive to sensory stimuli, because of a lack of inhibition of the stimulated reticular arousal system (see I.7). In our study we observed one animal performing a kind of "freezing" reaction to an unusual sound from an adjacent room at postnatal day 18: the rat pup sat motionless for one second only. However, the activity could alternatively be interpreted as a kind of orienting response, since it lasted for such a short time and was followed by upright sniffing.
At postnatal days 19 and 20 the social behaviour of the young rats was minimal. In all nests under study the animals huddled together in the nests throughout the observation sessions and, in fact, most of the day. It was very infrequent that a rat left the nest to walk outside or to eat at the feeding place, even inside the nest general activity was very low.
Animals raised under natural conditions do not leave the nest at the same age as the animals in our study did. Both wild norway rats (Calhoun, 1962) and rattus rattus (Ewer, 1972) were first observed outside the nest on the 21th postnatal day. Ewer observed the young animals to be very active inside the nest in the period preceding emergence.

Comfort behaviour

In the transition period, scratching, which was the predominant activity during the neonatal period falling within this category, did not occur more often. The number of times this behaviour element was observed remained stable. At postnatal days 19 and 20 scratching decreased along with the "dip" in general activity and was observed very infrequently. Washing, another element of this category, did increase during the period. This increase may reflect the enhanced ability of the young animals to keep their balance while sitting on their haunches. The animals were observed to be already capable of washing their faces for a few seconds at least. It was not quite clear whether such washing bouts were terminated by an inability to maintain a stable position for longer periods, or by the distracting hyperactive behaviour of littermates running or wrestling nearby.

Grooming, the third type of cleaning behaviour observable for the first time just prior to the beginning of the transition period, sharply increased during the transition period. It became the predominant activity in the category "comfort behaviour" by days 17 and 18. Again this increase was probably due to the enhanced ability to maintain the upright sitting posture which is the favourite position for grooming the fur.
A decrease in total time spent in washing and grooming occurred at days 19 and 20 although grooming was still observed for a considerable amount of the time.

Locomotion

At this stage crawling has almost ceased altogether and become transformed into coordinated walking. Walking was almost always accompanied by sniffing movements of the nose. Thus the score under the heading walk also includes the time spent on exploratory walking progression. As already mentioned, the behaviour of young rats during the middle of this period included spasms of hyperactive behaviour. Walking progression sometimes alternated very suddenly with brief flurries of exaggerated locomotor activity e.g. dallying and turning. These activities, often referred to as playful, appeared for the first time during the transition period. Dallying, i.e. sudden undirected frantic running around through the cage, seldom lasted for more than a second, and was often terminated by the animal dashing into a littermate. Turning, i.e. a sudden turn and rapid running movement in the opposite direction, again did not last for more than a second. Both activities gave the impression of spontaneously occurring, playful locomotory activities. They were, however, not exclusively performed by young animals. During the observation days occurring in the subadult period, when the animals had reached an age of 75 and 90 days, these elements were also occasionally observed. Although frequency of performance had decreased to a very low level, they had not disappeared altogether. Even adult rats were also seen performing playful activities at times. Climbing, another element in the locomotion category, was scored for the first time in the transition period too. One animal was seen climbing the nest boxes as early as postnatal day 16. By the 17th and 18th day most of the animals were seen to be doing this. Climbing was performed somewhat awkwardly and did not become a skillful performance until the onset of the socialization period.

Exploration

Following the decline, early in the transition period, a sharp increase in exploratory sniffing behaviour was observed at days 17 and 18 postpartum. According to Welker (1963), the 18 days old rat displays a fully developed sniffing repertoire, all four components being functional at the adult level. The four activities have been integrated in a fixed temporal organization and have reached adult rates of performance. Due to the development of balanced rearing behaviour, the young animals often sniffed the air while standing upright. Exploratory sniffing lasted a few seconds only. The decline in general activity was reflected by a considerable decrease in the amount of time spent on exploratory sniffing over the last two days of the period.
Other behaviour activities that were observed to emerge during the transition period were digging in the shavings, gnawing the wooden walls of the nest boxes and drinking at the water tubes. One animal was once observed throwing shavings into the air.

Towards the end of the transition period the behavioural repertoire has extended to some 35 distinguishable elements. By the 20th day the animals possess a fully developed adult motor equipment. At the sensory level audition and vision become fully functional. The animals still spend most of their time inside the nest, where they are usually very active. Animals emerging from the nest display bursts of hyperactive behaviour in the form of high-intensity and playful solitary activities. These bursts of activity end as abruptly as they begin. At this time the first social behaviour activities were observed.
A remarkable occurrence was the appearance of a "dip" in activity of the litters on postnatal days 19 and 20. Small (1899) and Bolles and Woods (1964) reported the same phenomenon. In their studies this decline occurred at approximately the same age. Small suggested that the observed inactivity could be due to the fact that the young pups had not been suckled that day, since the mother had escaped from the cage the night before. Bolles and Woods also hypothesized that the absence of the mother caused the effect. They weaned their pups at the age of 21 days.

Both explanations seem inadequate in accounting for the observed inactivity in our study. Since in this study weaning took place on the 30th postnatal day, the explanation for the causation of the phenomenon must be sought elsewhere. We are inclined to attribute the decrease in activity to maturation processes within the C.N.S. of the young organisms. Some developmental changes in neuro-anatomical structure and neurophysiological functioning may account for the "dip" found in activity (vide infra).

I.3.3. The Socialization period (21-30 days)

General information

The change in social behaviour which takes place in the socialization period is remarkable. The young pups suddenly begin to leave their nests and spend progressively more time away from the mother until, towards the end of the period, weaning appears to be complete. The mother gradually spends more time sleeping alone and in fact tries to avoid the young rats. The pups become more and more engaged in social contacts. Immediately upon walking out of the nest they show a gradually increasing and uninhibited interest in the environment and in their littermates. The age at which all our young pups left the nests is in accordance with the observations of Calhoun (1962) and Ewer (1972) on wild rats living in natural habitats. Wild rats do not leave their nests before 22 days of age (rattus rattus; Ewer) or 20 days of age (rattus norvegicus; Calhoun). According to Calhoun, the wild norway rats do not make their first explorations out in the open before the 24th postnatal day. Before that age they eventually leave the nest but remain in the burrows. Our seminatural environment with relatively "open" nesting places is probably more similar to the nest shelters of the rattus rattus, a species which nests in trees. A remarkable change in the behaviour of the mother, simultaneously with the emergence of the young from the nests, was noticed by Ewer. The mother, very aggressive during the earlier periods and attacking anything moving in the vicinity of the nests, becomes very tolerant as soon as the young begin to walk out. The inhibition of aggressive behaviour probably prevents her from attacking her own young.

Within the frame of our study the socialization period appeared to be a period characterized by the emergence of many new behaviour patterns or postures, most of which are related to social encounters. At the end of the period the repertoire has extended to some 55 elements and seems to be complete except for high-intensity attack and fighting elements as well as functional sexual activities. The social encounters between littermates were very frequent and performance was characterized by "hoppy" motor behaviour. Behaviour activities were extremely short-lasting and the behaviour changed in unpredictable ways. A typical sequence might thus be as follows: animal grooms, jumps, digs, kicks, jumps at a littermate, fights, explores, investigates and climbs. All these activities are performed within a few seconds often in an incomplete fashion. Observation of ongoing behaviour during the socialization period was therefore a very difficult task. Animals were frequently observed to change their activities three times in a single second. In such a case a choice had to be made by the observer, but obviously in making a selection of one out of the three activities the results necessarily become biased. Although tapes were recorded over and over again and in each case the most prominent activity was jotted down, a subjective decision was after all inevitable in each case. Detailed investigation of high-speed motion pictures or videotapes, frame by frame,makes possible the unravelling of the complex intermingling of various activities, performed at a rate that would produce insoluble problems for the human observer devoid of adequate technical facilities. Continuous direct observation of the rapidly changing activities therefore displayed some characteristics of a time-sampling method, at least in the socialization period.

The interactions occurring between littermates were also unpredictable. The young reacted appropriately and unreliably to the behaviour of the partner. Activities seemed to be motivated primarily by spontaneous fancy rather than being elicited and adapted to the littermates' performance. Although dyadic interactions were predominant, the young quite frequently engaged in multiple interactions. Occasionally all six animals were involved in the same activity at the same moment.

There were no signs of role taking behaviour during the period. The time spent on various activities did not differ significantly between males and females.

No indications of the establishment of a dominance hierarchy could be detected

between males. Rapid switching of the activities, characteristic of dominance or submission sometimes occurred within one and the same animal. Apparently neither sex-role nor dominance status are major determinants of the behaviour in the socialization period.

The manner in which young animals of this age conduct themselves has been termed "playful" by a number of students of the subject (Small, 1899; Bolles and Woods, 1964; Calhoun, 1962; Barnett, 1963; Ewer, 1972). A distinction is usually made between solitary locomotor play and "rough and tumble" fighting play. Although the impression of a lack of seriousness in performance is rather subjective (Hinde, 1970), and the concept of play is not a scientifically useful explanatory concept (Welker, 1971; Millar, 1970), the behaviour of young animals certainly bears some characteristics which distinguish it from adult behaviour, and may justify the use of the expression "playful":

a) the tempo of performance is very fast and the distinct activities exhibit a short duration time,
b) behavioural sequences are incomplete and unpredictable, mixed patterns of different functional systems occur,
c) patterns or postures are often performed in an incomplete and fragmentary fashion. For instance, fighting is not accompanied by components such as piloerection, teeth chattering or biting,
d) some patterns, seen in the adult, do not occur in the playful behaviour of young rats. In our study the "appetitive" elements of the fighting sequence such as threat and sideways offensive posture were absent. Freezing alternatively known as the cataleptic posture occurring in adults often as the result of vigorous fighting was also lacking,
e) interactional performance was not "tuned" to the behaviour of the partner.

It should be stressed, however, that behaviour patterns exclusively performed by young playing rats were not observed. The sequences of playful behaviour appeared to consist of motor patterns normally employed in various functional contexts by adult animals. Qualitatively, the behaviour of young rats during the socialization period exhibit striking similarities with that of young developing domestic

junglefowl (Kruyt, 1964). During the first stage of social development Kruyt observed shortlasting, frequently changing behaviour elements belonging to the adult aggression or flight inducing motivational systems.
Actual performance throughout this developmental stage seems to reflect the imbalance existing between the tendency to attack and the tendency to flee. The observations conducted during our study are, however, insufficiently accurate to validate the general applicability of such a hypothesis. Besides this, it is possible as Hinde (1970) has suggested, that motivations present in young animals but absent in adult rats, may be responsible for playful behaviour.
Another point which deserves attention is the sequential development of behaviour elements. A point which became clear from qualitative observations and was further supported by quantitative data, was that elements of behaviour development properly belonging to the end of a behaviour sequence are often the first to occur. Thus the so called "consummatory" motor patterns generally appear earlier in ontogeny while the normally preceeding "appetitive" patterns appear later. For instance it was noticed that in washing, scratching and grooming activities the consummatory motor patterns were already present before the appropriate postural skill had developed and functional proficiency achieved. In the playful behaviour shown by young rats, elements belonging to the end of the aggressive behaviour sequence (fighting and lying down) or of the sexual sequence (mounting and clasping) were observed to appear before the introductory elements did (sideways defensive posture, upright posture, anogenital inspection and following). Bolles and Woods (1964) also noted that during the socialization period the appearance of various kinds of defensive behaviour follows that of the offensive agonistic activities. The exact manner in which simple behaviour elements become metamorphosed into adult spatiotemporally complex sequences, and how the appetitive and consummatory activities become integrated and organized, remains a still unanswered question which urgently needs investigation.

Social behaviour

On leaving the nest, the young pups come into social contact with littermates. Qualitatively speaking there follows an obvious development in these contacts. During the first days of the socialization period encounters seem to be more or less accidental, being brought about by the uninhibited hyperactive locomotor activities of the young. Gradually, the contacts were observed to become more directed: animals actively sought littermates or were elicited by them to engage in social encounters. Throughout the period the rate of performance was very high. Animals were very "jumpy", the very frequent and brief social encounters being performed with excessive motor performance. This redundancy waned more and more, as the animals gained enhanced motor behaviour through practice. Fighting was the predominant social activity observed, but while this was performed rather vigorously it never seemed to be serious. Animals tumbled over each other turbulently, and squealing sounds were detected, but there were never any signs of wounding. Moreover a fight never resulted in freezing behaviour. A fight might end by one animal keeping the partner down, but the animal lying underneath never submitted but always tried to free itself by squirming, striking and kicking with fore- and hindfeet. A moment later, the pup, righted, would be keeping down the other pup. The interactions were extremely variable and often more than two animals were observed to engage in social fighting contacts. The fights might start by one animal actually jumping at the partner. Such violent, uninhibited frontal attacks are very seldom observed in adult animals, except in interspecific encounters. During the socialization period they appeared rather frequently. The antagonistic upright postures, standing attention and standing upright boxing, were present but were not seen very frequently. When one or two animals simultaneously adopted this position, it was never maintained for a long time. The postures are thought to be "ambivalent" ones: they can be performed by rats in a defensive or an offensive context. Detailed observation of additional features such as piloerection, flattening of the ears, protruding or closed eyes, is necessary to decide on which "mood" the rat is in. This additional information could not be obtained, because the signs were still absent. Possibly the activities

do not yet possess any functional significance in either direction.
A social defensive element, which at first appearance seems to lack any functional properties, is kicking (fig. 6). In the socialization period it reaches a high frequency. However, the behaviour elements with which it is very often linked among interacting adult rats (anogenital inspection and mounting) occur infrequently at first. The activity was performed very often by solitary animals, but gradually this inappropriate orientation changed and it was used in social contexts against animals investigating, following etc.

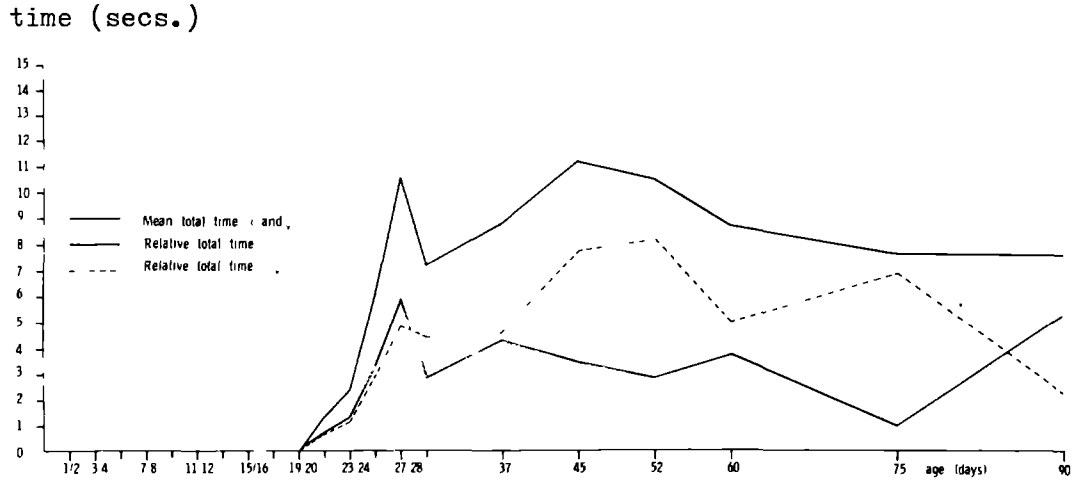


fig. 6. Kick. Total time spent on kicking behaviour at various days of age.

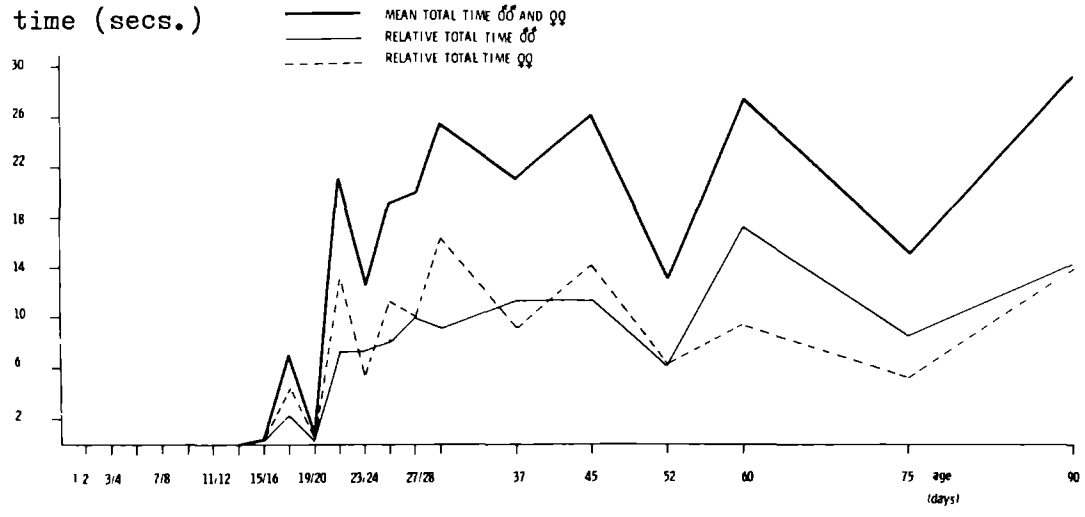


fig. 7. Investigate. Total time spent on investigating a littermate at various days of age.

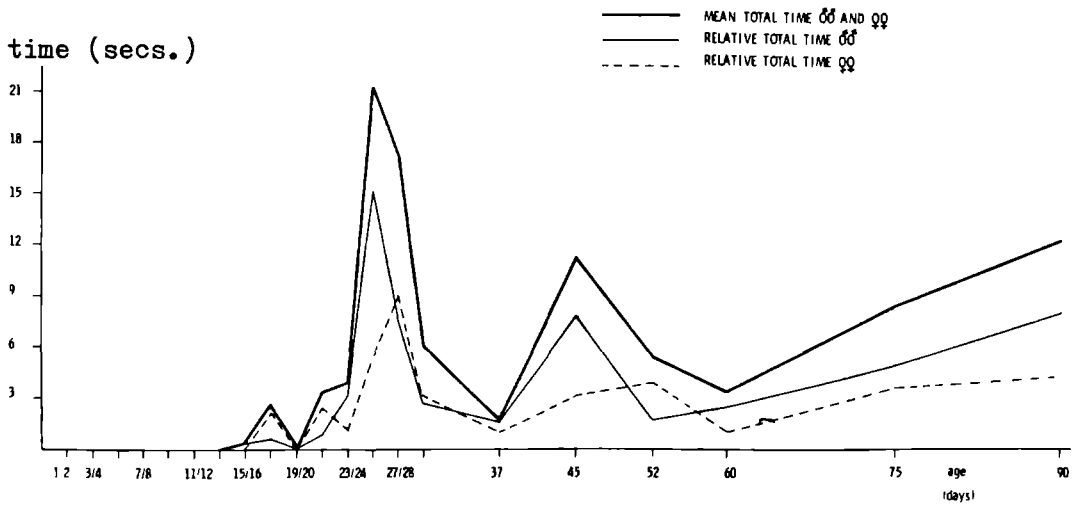


fig. 8. Social grooming. Total time spent on social grooming at various days of age.

The social exploratory behaviour elements became complete during the socialization period. Investigation of the partner gradually increased and eventually reached a high frequency (fig. 7). Quantitatively, the amount of time spent on investigation did not significantly change with increasing age, but there was however, a qualitatively difference. During the transition, socialization and early juvenile periods, investigation was superficial and short lasting while in subadult and adult animals investigation was more thorough and was continuously performed for longer periods of time. Nosing, the brief simultaneous contact of the noses of two animals, as well as oral inspection did emerge. The latter element can be observed quite frequently during the same period in mother-young interactions. Ewer (1972) hypothesizes that the young are attracted by the smell of saliva and that the activity of saliva licking may be instrumental in the transition from nursing to eating solid food. Anogenital inspection was observed very late, occurring rather infrequently during the socialization period, and apparantly lacking any functional significance as yet. It was not sequentially linked with mounting behaviour which itself increases towards the end of the socialization period.

Mounting during this period consisted of clasping the partner and bringing the belly into contact with the body. Orientation was poor, animals often mounting onto the partner's head or side. Pelvic thrusting was also lacking completely. By the middle of the socialization period, grooming a partner became a generally performed activity (fig. 8). Social grooming reflected the characteristics of the normal behaviour of the animals during this period: pups groomed each other very vigorously, pushing their nose into the partner's body with great strength. This kind of performance is identical to what in adult rats is referred to as aggressive grooming (Grant, 1963; Timmermans, 1977). Although the partner might make squealing sounds, grooming never develops into serious fighting or submission during the socialization period. The sideways defensive posture, frequently observed in adult rat encounters, also emerged in this period. As may be said of all the activities, this posture often appeared in an incomplete, abbreviated form, and,if animals were sitting or walking,was difficult to distinguish from kicking or keeping off. Striking, retreating and following, activities which emerged during the transition period displayed an increase in performance. The high score found for strike was probably partly induced by the environment, which, as already mentioned, favoured performance of this activity.

The above remark is also true for pulling behaviour. Animals would try to pull a littermate out of the nest compartment often by tugging them by the ears. During the socialization period huddling gradually decreased to a low level because the young pups spent progressively less time inside their nest compartments.

Comfort behaviour

The time spent on all cleaning activities taken together, increases immediately after the onset of the socialization period. A peak was reached at days 25 and 26; thereafter a slight decline occurred.
Grooming remained by far the predominant activity. Washing and scratching were observed fairly often, although an increase in total time spent on these activities occurred in comparison with that during the neonatal and transition periods. Washing and grooming had developed into skillfully performed activities and were

sometimes observed occurring sequentially as in adult animals. During the socialization period a washing or grooming bout was usually terminated by a littermate seeking social contact and, thereby, distracting the animal engaged in cleaning behaviour.

Locomotion

The hyperactivity of the young rats during the socialization period is reflected by a sharp increase in frequency of already existing motor behaviour patterns, together with the emergence of new ones.
Walking showed a very sharp increase and, in fact, reached a peak on day 27 (fig. 9).

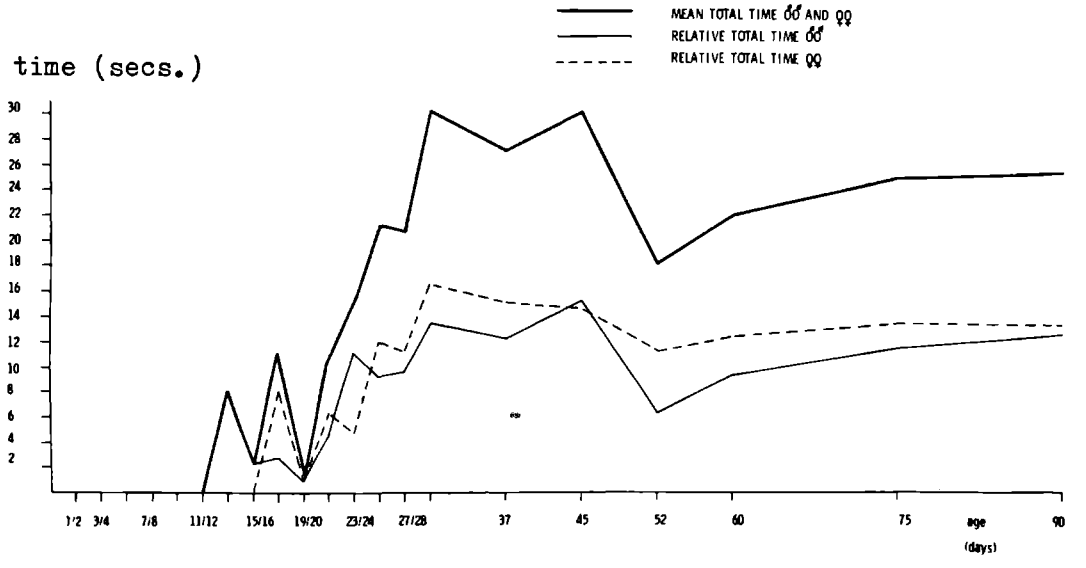


fig. 9. Walk. Total time spent on walking at various days of age.

After the 30th day the animals spent less time walking than the young did during the socialization period. As can be seen from the graph, there was at no time any difference between males and females with respect to walking.
The rats spent more time in the playful frantic locomotory patterns dally and turn, which were first observed in the transition period. Dallying became a favourite activity.
New locomotion patterns or motor patterns emerged: jump, run and hop. Jumping became very general. Sometimes it occurred spontaneously, the animals jumping vertically in midair. Jumping often preceded running or dallying. Hopping performed as a solitary activity was seen infrequently. Social patterns or postures such as retreat, follow or fighting were performed in a "hoppy" or "jumpy" way. The redundancy in motor behaviour was one of the main characteristics of overall performance during the socialization period.
More time was also spent on climbing the nest compartments and food hoppers and occasionally a rat pup would even try to climb the sidewall of the cage.

Exploration

Sniffing at anything in the environment was a favourite activity. Exploration bouts were very short, interrupted by social or grooming activities. The amount of total time spent on exploration reached a peak at the end of the socialization period, by which time it was by far the predominant activity as indeed it continues to be throughout adult life. Once again, no difference whatsoever could be detected between males and females in respect of exploratory behaviour (fig. 10).

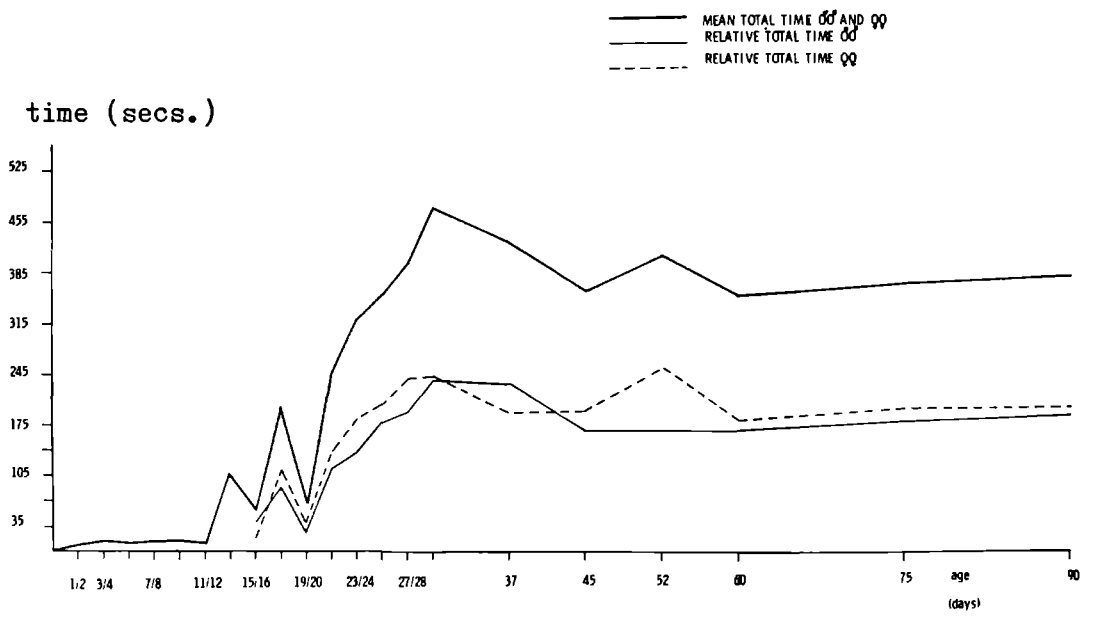


fig. 10. Exploration. Total time spent on explorative behaviour at various days of age.

By the end of the socialization period the young rat has developed a repertoire of social behaviour which is almost complete. However, what is remarkable is the lack of the introductory, threatening elements of the aggressive sequence. Those activities which in adults reflect fear or caution, such as freezing, crouching, or the cataleptic posture are also absent. Apparently fighting is still not a serious activity. Rudimentary sexual activities emerge but orientation is still poor.

In our study the mother was removed at the 30th postnatal day and the environmental space was extended to twice the original size.

I.3.4. Some remarks on the development of the central nervous system in the rat.

Several authors have stressed the importance attaching to knowledge of neuro-anatomical, neurophysiological and neurochemical ontogenetic data for students of behavioural ontogeny (Eayrs and Goodhead, 1959; Bronson, 1965; Hamburger, 1968; Bekoff and Fox, 1972). Data gathered by observation at the behavioural level may

be explained by additional information stemming from studies of postnatal neural development. The processes of neurogenesis and genesis of behaviour cannot be thought of as separate uncorrelated events. For this reason a limited review of the ontogeny of the CNS seems appropriate.

The newborn rat comes into the world with a very immature brain. At birth the total number of cells in the neocortex is only 50% of the adult number. By some 14 days postpartum the percentage has increased to 90%.

Berry (1974) makes a distinction between the processes of neurogenesis and gliogenesis. According to him neurogenesis in the neocortex has almost ceased before birth. Only in a few areas of the CNS -the brainstem nuclei, the hippocampus, the olfactory bulbs and the cerebellar cortex- does neurogenesis continue into the postnatal period. Postnatal neurogenesis in these areas is exclusively concerned with microneurons: small cells with very short axons terminating within the structure in which their cell bodies are located. In the rat, large neurons are formed postnatally in the caudate nucleus, the putamen and the accumbens septal nucleus.

The macroneurons or Class 1 neurons, most of them formed prenatally, are thought to develop under genetic control and to possess invariant structural and functional characteristics (Jacobson, 1974). The axons of the macroneurons are very large and constitute the afferent and efferent pathways of the CNS. The microneurons, developing later in ontogeny, connect locally and are thought to subserve integrative functions between the primary afferent and efferent systems. Jacobson (1974) believes that the microneurons possess greater plasticity and that environmental influences are very important in the process of differentiation of these neurons.

The investigations of Eayrs and Goodhead (1959), using the reduction of the cell packing density as a parameter of brain maturation, revealed a rapid reduction in postnatal cell packing density. Following the end of the first week an increase in the number of dendrites arising from the perikaryon was found, the total number reaching adult values by the 12th postnatal day. After the 12th day of age an increase in peripheral extension and branching of existing dendrites occurs. The most rapid increase was discovered during the period between 18 and 24 days. Changes in the length of dendrites continue into adult life.

At birth very few axons are present. The induction of axon formation is a first step in cell differentiation and begins soon after birth. The most rapid increase in the density of axons (6-18 days) precedes the increase of dendrites. According to Eayrs and Goodhead, by the age of 18 days the cerebral cortex possesses all the qualitative adult-like properties; all layers are present and well defined. The changes occurring between this age and maturity are quantitative rather than qualitative.

The process of gliogenesis begins perinatally and continues into adult life. Astrocytes are the first to appear; oligodendroglia appear just prior to the process of myelination of the tracts in the CNS (Berry, 1974). Myelination of the cerebral axons begins at about the 10th postnatal day, concomitant with the development of oligodendroglia.

Myelination proceeds successively: the sensory projection fibers myelinate before the corticofugale fibers, the medulla, pons and midbrain myelinate earlier than the thalamus and the cerebral cortex. Cerebral axons in the motor, somesthetic, auditory, limbic and pyriform cortex are the first to myelinate. Neighbouring regions are next to myelinate and the visual sensory regions are the last. Since specific stimulation is able to evoke responses from cortical structures not yet myelinated, the view that a causal relationship exists between myelination and the acquisition of function must be rejected. The process of synaptogenesis and (probably) the maturation of peripheral sensory receptors are of the utmost importance for the functional integrity of the CNS (Berry, 1974).

At birth there are very few synapses, most of these being axodendritic. From postnatal day 19 a rapid increase in the number of synapse may be observed. By day 22 postpartum, an increase in axosomatic synapses in the rat was found, and their number had reached adult values by the 30th day. Synapses have excitatory and inhibitory functions. Since there is evidence that excitatory areas in the brain develop earlier than inhibitory areas do (vide infra), axodendritic synapses were thought to subserve excitatory functions and axosomatic synapses to subserve inhibitory functions. Recent investigations by Crain (1974) on the development of inhibitory circuits in the CNS indicate, however, that this distinction is probably incorrect. Crain found that even as early as in the embryonic period, inhibitory

systems might be active. Bioelectrical inhibitory post-synaptic potentials could be obtained prenatally from very primitive synapses.

The area of the cerebellum, a structure involved in the coordination of complex body movements, postural adjustments and skilled motor performance, increases twenty-fold during the first 3 postnatal weeks, due to growth of the cerebellar cortex (Altman, 1969, quoted by Bekoff and Fox, 1972). There are three periods of accelerated maturation: at 1-3, 9-12 and 16-19 days of age. The period 9-12 days is marked by a large increase in protein synthesis in the cerebellum. According to Bekoff and Fox, the duration of cerebellar neurogenesis (the first 3 postnatal weeks) seems to correlate with the period necessary for the maturation of locomotor and related skills in the rat. This suggestion is supported by the results of our study. Moreover, it is interesting to note that periods of accelerated maturation of the cerebellum are concomitant with accelerated improvements in locomotion and related skills. Bioelectrical E.E.G. activity can be detected in the cerebral cortex as early as day 5 postpartum. By the 10th postnatal day the E.E.G. can be detected without any difficulty (Crain, 1952). From day 15 onwards the E.E.G. develops rapidly and exhibits the adult pattern of activity at about 30 days of age (Deza and Eidelborg, 1967).

Although the mediating structure underlying the electroencephalographic activity is present as early as 10 days of age, it seems doubtful that the cerebral activity has functional significance to the behaviour of the animal (Berry, 1974). Salas et al. (1969) were able to detect spontaneous activity in the olfactory bulb at the age of 3 days. A rapid increase in frequency and amplitude of bursts was found between the 4th and 12th postnatal day, contingent upon the process of microneural cell proliferation in the area. By the 12th day the olfactory bulbs reach the adult-like laminar organization, although cell differentiation continues until about the 20th postnatal day. By the 24th day postpartum the electrical activity reaches adult frequency values. Despite the lack of spontaneous olfactory bulb electrical activity during the immediately postnatal period, Salas et al. do not exclude the possibility that animals of that age respond to olfactory cues, as some other authors have suggested (Small, 1899; Welker, 1962; Tobach et al., 1967). The electrical activity may be below the threshold of sensitivity of the apparatus used.

Another possibility which cannot be excluded is the appearance of electrophysiological changes in other areas of the CNS following olfactory stimulation, for instance the early maturing formatio reticularis.
Salas et al. obtained the first spontaneous electrical activity in the visual cortex by the 4th postnatal day. At the 12th postnatal day, just before the opening of the eyes, adult-like activity patterns emerged.
Efforts to correlate behavioural ontogenetic data with findings on the development of neuroanatomical structure and neurophysiological functioning of the CNS have been made by Fibiger et al. (1970), Moorcroft (1971), Moorcroft et al. (1971), Campbell and Mabry (1972) and Oakly and Plotkin (1975). The behaviour parameter used in these studies was spontaneous locomotor activity, as measured in a stabilimeter cage. The spontaneous locomotor activity appears to be low for the first 10 days postnatally and shows a sharp increase beyond that age. Between 15 and 20 days of age the activity reaches a peak. Spontaneous locomotor activity beyond the age of 20 days declines rapidly to adult levels shortly before 30 days of age (Moorcroft et al.,1972; Oakly and Plotkin, 1975). The investigators relate the behavioural data to the sequential caudal-rostral development of brain structures. Caudal structures, brainstem and mesencephalon, mature first and approach adult levels of development at the end of the second and beginning of the third postnatal week, as judged by myelination, bioelectrical activity and concentrations of neurotransmitters. The peak in locomotor activity thus parallels the development of excitatory structures in the CNS, notably the structure responsible for arousal: formatio reticularis.
More rostral structures, diencephalic and telencephalic areas mature relatively late in development. These areas are thought to be inhibitory centres and they affect behaviour by inhibiting lower excitatory caudal centres. The forebrain inhibitory centres are not functional until after the third week of life. Moorcroft (1971) was unable to find an inhibitory effect of the hippocampus before 21 days of age. The frontal cortex did not attenuate behavioural arousal before the 23rd-26th postnatal day.
Fibiger et al. (1970) also correlate the neuroanatomical data with psychopharmalogical findings. The development of the adrenergic arousal system and the cholinergic inhibitory system is contingent upon the sequential neuroanatomical development. The adrenergically mediated arousal system is functional at birth or

shortly thereafter. The antagonistic cholinergic inhibitory system appears to develop gradually between 20 and 25 days of age. Douglas et al. (1973) found that young rats are not capable of spontaneous alternation behaviour before about 27 or 28 days of age. It is believed that spontaneous alternation as a form of unlearned behaviour is related to the inhibitory function of the hippocampus and the cholinergic system. In order to function in an adult manner, the maturation of the hippocampal structure must be complete. They conclude therefore that the maturation of the inhibitory cholinergic system is not complete before the 4th postnatal week. In comparative ontogenetic studies of both precocial and altricial animals, Campbell and Mabry (1972) as well as Oakly and Plotkin (1975) were able to confirm the picture presented above. Oakly and Plotkin state that in the life of the rat, postnatal day 20 is the point of transition from mesencephalic to diencephalic and telencephalic maturation. In this connection, a finding of Sedlacek et al. (1961) quoted by the authors is of interest. Sedlacek et al. report that the transition from mesencephalic to diencephalic phases of maturation is marked by a temporary inhibition of already established reflexes to skin stimulation such as washing and licking. The transition and correlated temporary inhibition may be an explanation for the "dip" in behavioural activity found during our study. Although we observed a sharp increase in activity between 15 and 20 days of age, this increase was not followed by a decrease as was the case in the studies mentioned before. On the contrary, a gradual increase in overall activity, as measured by the number of different behaviour elements per unit time, was observed after the 20th postnatal day, reaching a peak at 37 and 45 days. The discrepancy between our results and those of Moorcroft et al. (1972) and of Oakly and Plotkin (1975) may be due to the fact that these authors measured only a particular kind of locomotor activity in a very restrictive environment. It should be clear from this review that a newborn rat is a helpless creature endowed with very limited behavioural equipment and a very immature brain. During the first 30 days of life, overwhelming changes occur. The 30 day old rat has already developed a nearly adult-like behavioural repertoire. Qualitatively, the CNS has also by that time reached adult-like proportions. There is no doubt that a complete interplay exists between developmental features observed at the behavioural level and the CNS level. It would be tempting to correlate behavioural

data gathered in our study with data provided by studies at the neuroanatomical, neurophysiological and neurochemical level. Occasionally we have made an effort to discover an explanation at a physiological level for a phenomenon, unexplainable at the behavioural descriptive level. It was beyond the scope of this thesis to perform such a task extensively. However, it was felt that problems arising in studies of rat development could be best tackled by various approaches to the process of development. Such a multidisciplinary approach would be extremely illuminating, as well as being of heuristic value to all workers in this field.

I.3.5. The juvenile period

General information

The transition from the socialization period to the juvenile period, is less well marked than the transition from the neonatal to the transition period, or from the transition to the socialization period. During at least the first half of the period the animals continue to behave hyperactively. Performance is very intensive and the animals almost incessantly engage in playful behaviour. They are increasingly attracted to engage in social contact with their littermates. In fact the amount of time spent on social activities reaches a peak within the juvenile period (fig. 11), but no new behaviour elements were observed. Only towards the end of the period did mounting behaviour develop into its adult functional form: orientation was correct and pelvic thrusting was present.

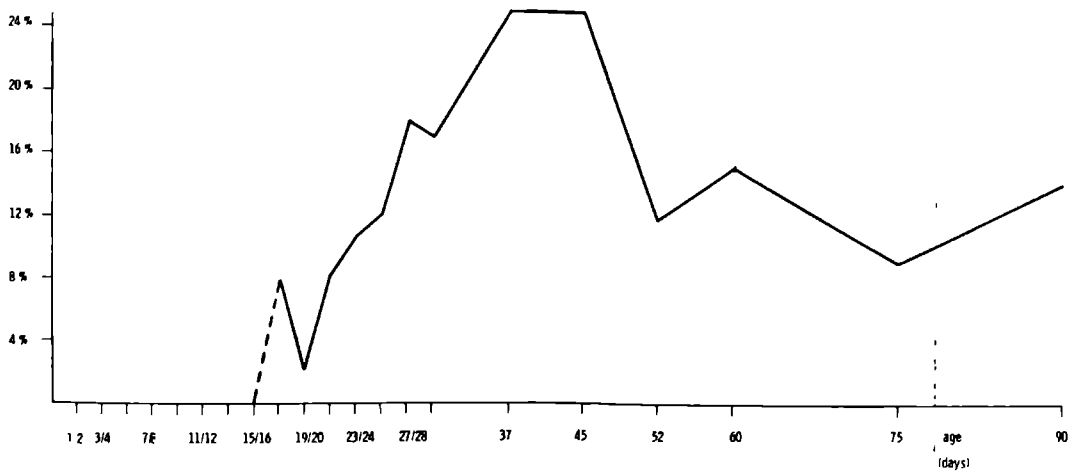


fig. 11.. Social behaviour. Total time spent on social behaviour at various days of age.

There are several reasons to set the onset of the juvenile period at about the 30th postnatal day. First of all the young rats become completely self-supporting by that time since weaning is complete. Moreover, wild rats living under natural conditions first come into contact with rats other than their littermates at about the age of 30 days. Thirdly, the structural maturation of the CNS is in many respects complete, and the CNS has become anatomically adultlike by about the 30th postnatal day. It should be stressed, however, that the division of rat development into periods is a rather subjective and arbitrary decision. Looked at behaviourally, the juvenile period can be divided into two distinct subperiods. During the first two weeks the behaviour of the young rats displayed characteristics identical to those of the socialization period. Quantitatively speaking, several social behaviour elements increased and reached a peak on observation days 37 and 45, while qualitatively, an increase in skilled performance of these activities could be readily detected. These activities appeared to be more complete and gradually most of the components of the adult patterns or postures were present. The expressive signs of high-intensity aggression, however, continued to be completely lacking. Observation of distinct elements thus became easier and somewhat less "hazardous", because more building blocks, characteristic of a behaviour element were able to be distinguished. The behaviour elements became more and more integrated into the functional adult sequences, although occasional interruption of these sequences by sudden unpredictable and jerky movements continued to occur. What is needed is an adequate technique of sequential analysis which would make it possible to transform these inductive and inevitably subjective observations into valid qualitative statements.

Soon after the 45th day of age the performance of behaviour changed rather abruptly and achieved the characteristics of adult performance. On the 52nd day a marked decrease was observed in rate of performance. The accelerated, abbreviated type of behaviour activity had settled into the calm and regular behaviour of adult rats. The amount of time spent in social behaviour decreased sharply as did the index of changes in behaviour also (fig. 12).

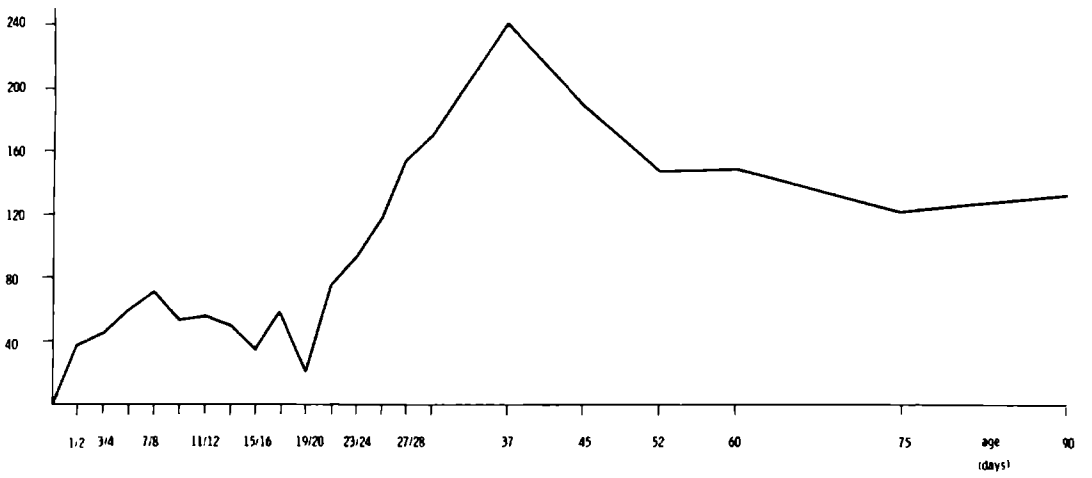


fig. 12. Mean number of different behaviour patterns in unit time

This implies that by this time animals are able to maintain performance of a behaviour pattern for longer periods. Integration of distinct elements into adult sequential patterns continued.

During the juvenile period the differentiation between the two sexes also became apparent. The differentiation was observed both in sexual behaviour and in agonistic encounters (vide infra).

It has already been established that the animals reach sexual maturity towards the end of the juvenile period. Females are thought to become sexual mature earlier than males. Calhoun (1962) reports in his study of wild rats that by postnatal day 55, 83% of the females had perforated vagina's, whereas only 13% of the males had their testes descended at that age. These percentages had changed to 94% and 40% respectively by day 65. Since in our study one female give birth to a litter as early as the 85th postnatal day, it is clear that at least one male had attained sexual maturity at about the 60-65th day of age. Dieterlen (1963) however, gives 79 days as an age when females become sexually mature.

Calhoun, in the above mentioned study, makes some remarks about the adult-juvenile interactions in rats, which have been confirmed by the studies of Barnett (1963)

in domestic norway rats and by Ewer (1972) in her observations of rattus rattus. Adult animals, both males and females are very tolerant toward young rats below the age of 45-50 days. Adults are often involved in playful interactions with juveniles in the same way as the juvenile-juvenile interactions. Lactating females begin to react aggressively to young animals after they have reached an age of 45 days. Occasionally adult males, engaged in transporting food or eating, show signs of mild annoyance when disturbed in their activities. The mildly aggressive reactions of the adults, or "psychological drubbing" (Calhoun) may be interpreted as functional to the process of social conditioning: juveniles must learn to inhibit behaviour patterns which are irritating to others. From about day 45-50 onwards the young rats gradually lose their immunity and are reacted upon aggressively by adult rats. However, they seldom show any signs of wounds before reaching sexual maturity. Wild rats tended to stay in close contact with both the mothers and the littermates throughout the juvenile period and were frequently observed in the vicinity of their nesting home.

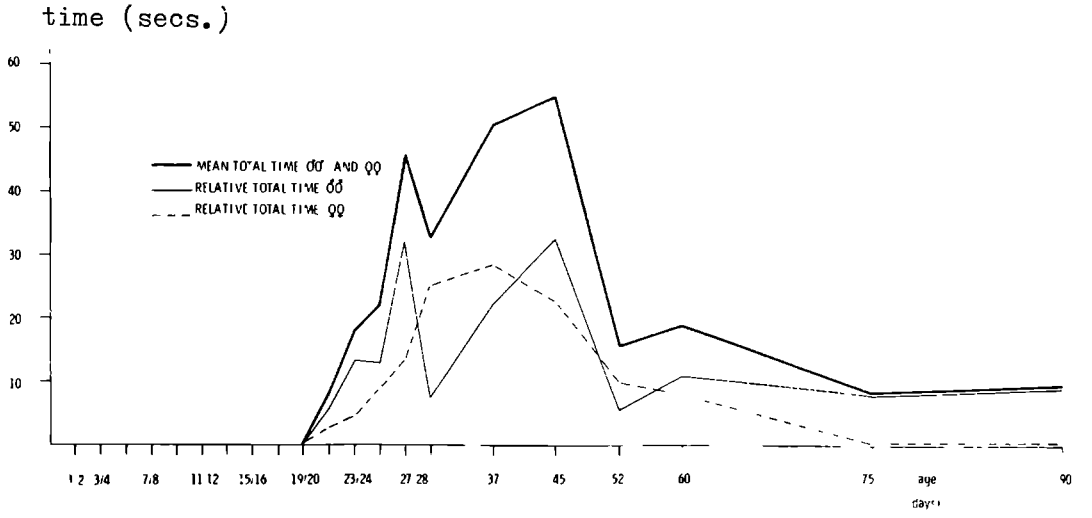


fig. 13. Fight. Total time spent on fighting at various days of age.

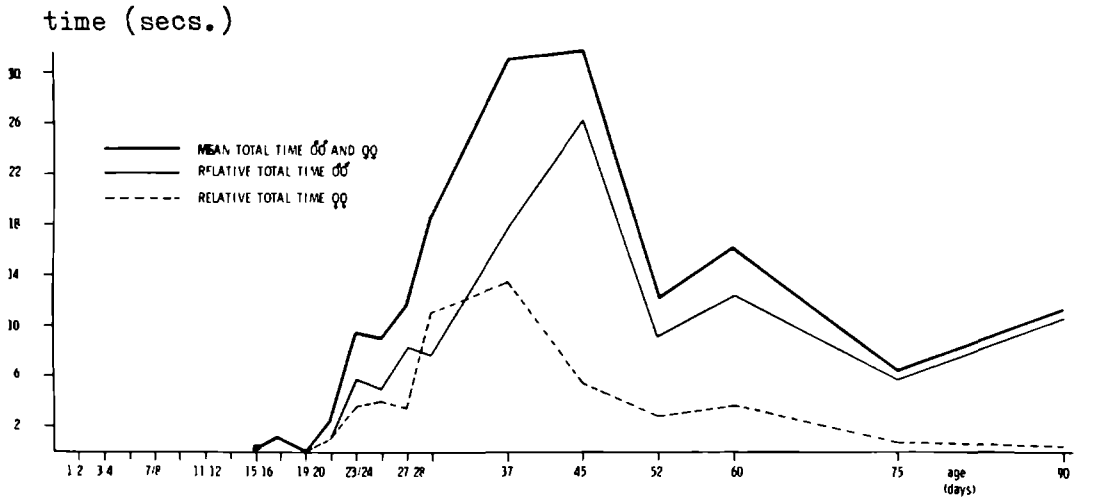


fig. 14. Keep down. Total time spent on keeping down at various days of age.

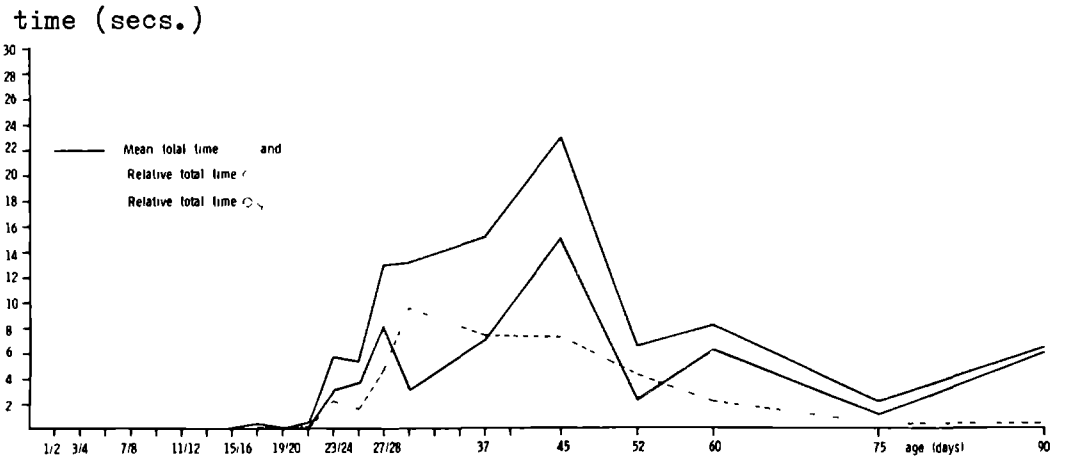


Fig. 15. Strike. Total time spent on striking at various days of age.

Social behaviour

Disregarding the "social" activities occurring inside the nest during earlier periods the total amount of time spent on social activities reached a peak on postnatal days 37 and 45. On postnatal day 37 the animals spent 24.9% of the observation time in social behaviour, and on the 45th day this percentage was 24.8% (fig. 11).

Later on in the juvenile period the percentage decreased to between 12% and 16%. From an analysis of the data, it may be concluded that the high percentages found for social behaviour were due to a sharp increase in the time spent on playful agonistic patterns and postures. Fighting and keeping down appeared to be the predominant social activities (fig. 13 and 14). During the juvenile period fighting was performed as often by males as by females, but in the subadult period when the animals had reached sexual maturity, females almost never were observed in fighting encounters.

The difference between males and females in dominating behaviour exhibits a different pattern. Even as early as day 45, males were spending by far more time in this activity, a trend continuing into later periods. This of course may mean that male-male interactions are prevalent and thus result in more dominating by male rats. Another possibility is that males in male-female encounters tend to be "winners" more often.

Among other "offensive" activities, "lunge" and "push over", reached their highest level of performance on postnatal day 37. The scores are an indication of the continuing uninhibited fashion in which the young juvenile rats interact in playful fighting activities. The mild agonistic activity "strike" showed an increase and reached a peak at day 45 (fig. 15). As already mentioned, this activity was performed more frequently by those animals which had climbed the nest compartments and followed this by making striking movements with the forefeet towards littermates also trying to climb.

On the defensive side the "keeping down" of one animal was responded to by "squirming", "keeping off in a lying position", or "rest". "Squirming" was the most frequently observed activity on day 37 (fig. 16). Animals remained in the

lying down position for a very short time only. During the juvenile period the picture changes. Keeping off becomes the prevalent activity somewhat later on day 45 (fig. 17).

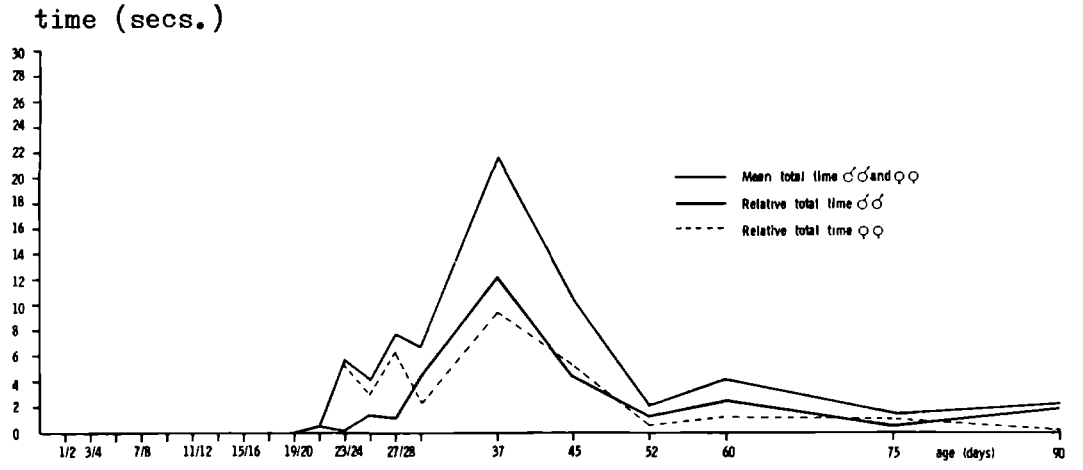


fig. 16. Squirm. Total time spent on squirming at various days of age.

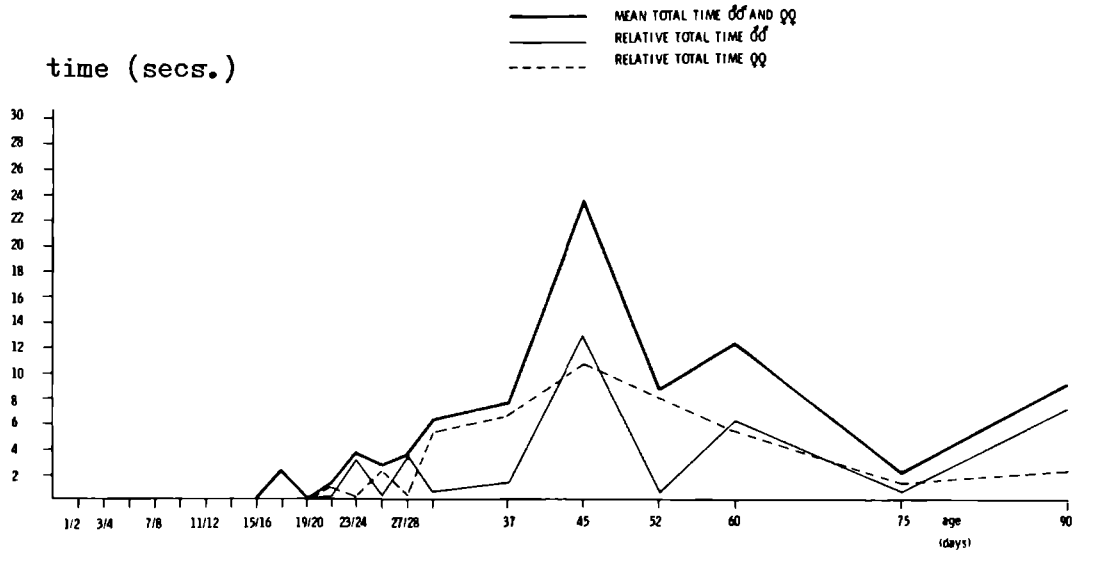


fig. 17. Keep off. Total time spent on keeping off at various days of age.

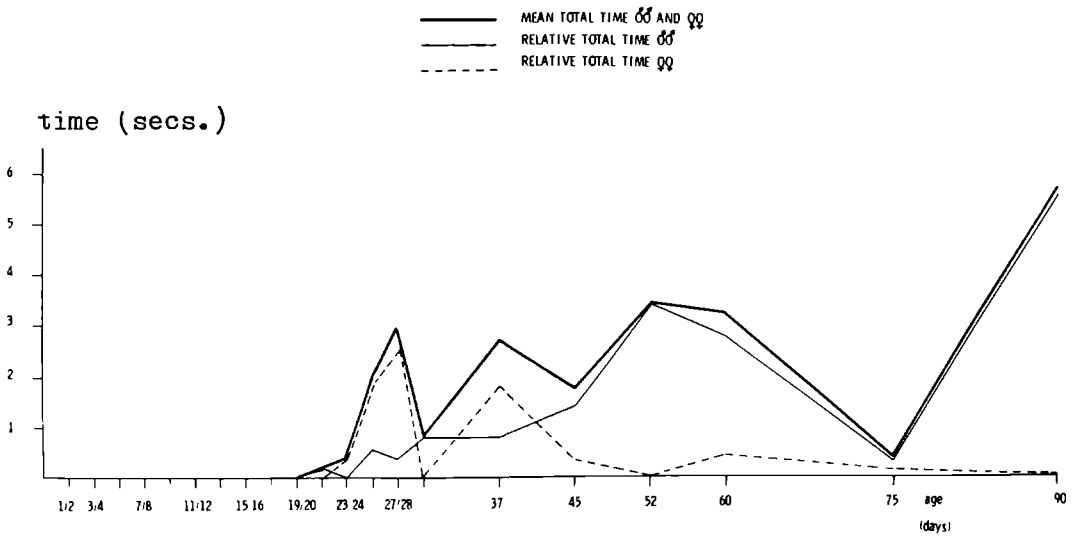


fig. 18. Box. Total time spent on boxing at various days of age.

At this stage the animals remain in the lying down position for longer periods of time continuously. Still later (on the 52nd day) the high incidence of resting may be an indication of an increased tendency to lie down motionless. No differentiation has been made however, between lying down when forced by a partner, and lying down spontaneously occurring. Both types of lying down have been scored under the heading "rest" and therefore any conclusion based on the quantitative observation of rest is purely speculative.
In future it would be wise to differentiate both qualitatively and quantitatively between the two types of lying down, and only then will a valid interpretation be possible. The agonistic activities, in which a rearing posture is involved (standing attention, upright posture, boxing) showed an increase during the juvenile period and became rather frequent at the end. Many fighting bouts terminated in the animals standing opposite each other and assuming a kind of boxing attitude (fig. 18). As can be seen, the onset of a differentiation between males and

females in respect of this activity occurs on day 45. Following this, boxing is confined almost exclusively to male rats. Since the activity is a symmetrical one, it may be concluded that male-male encounters sometimes result in boxing, whereas male-female and female-female interactions do not. The possibility that female-female or male-female agonistic interactions never occur has to be rejected: fighting was observed with equal frequency in both male and female juvenile rats. The relatively high incidence of boxing found on day 90 was the result of two animals engaged in a serious fight with each other (vide infra).

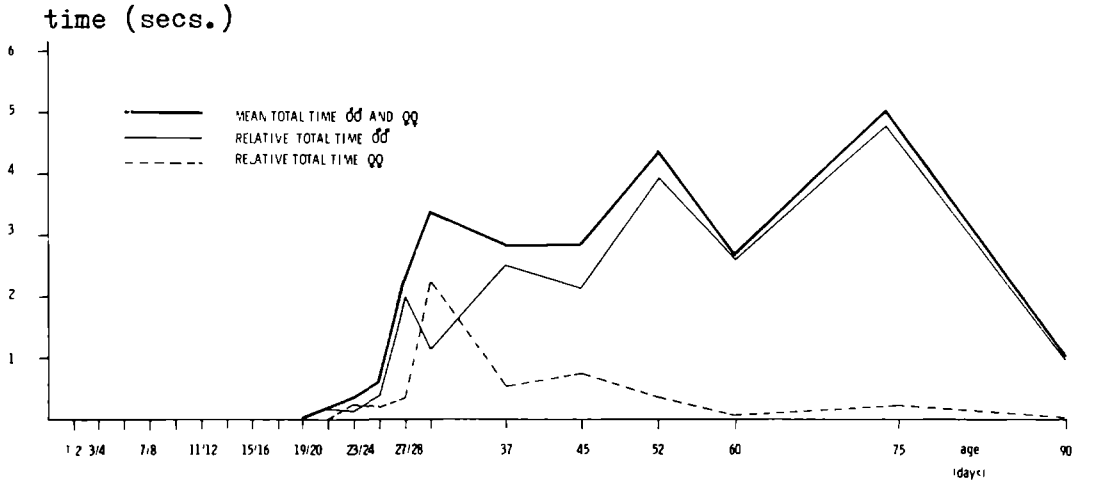


fig. 19. Mount. Total time spent on mounting at various days of age.

From our data on sexual development it may be concluded that the juvenile period is one in which the differentiation between males and females begins. During the preceeding periods, mounting behaviour including attempts to mount, had been performed more or less equally often by males and females. Differentiation was present as early as the 37th day (fig. 19) but from then on males were increasingly responsible for the amount of time spent on this activity. Mounting was rarely observed in females. Anogenital inspection, which in adults, is linked to mounting and often precedes it, showed a sharp increase within the juvenile period, especially after the 45th day. The pattern of development here is somewhat different from that of mounting. There is no differentiation between males

and females on days 37 and 45, but from day 45 onwards the differentiation emerges as may be concluded from fig. 20.

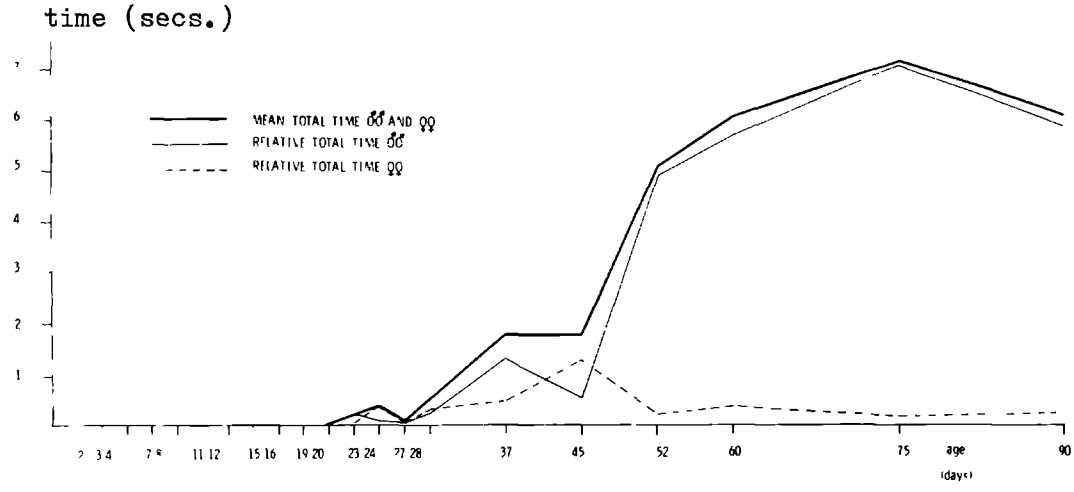


Fig. 20. Anogenital inspection. Total time spent on anogenital inspection on various days of age.

On day 52 the male juvenile rats accounted for almost the total time spent on anogenital inspection. The sequential association between the two seperate elements probably takes place towards the end of the juvenile period.
In the present study female sexual behaviour patterns (Timmermans, 1977) were not observed in detail. Among the reasons for this is the fact that the observations were insufficiently accurate to decide upon the functional properties of elements such as following and retreating behaviour.
It should be noted that the differentiation existing between males and females in behaviour patterns employing agonistic and sexual interactions seem to synchronize. Profounder and more detailed observations must be performed in order to find an answer to the question of the possible relationships existing between the two systems involved in agonistic and sexual interactions.

Comfort behaviour

An increase was observed in the different types of cleaning activities. Grooming showed a gradual increase and finally attained a high level of performance late in the juvenile period, after which it remained the predominant activity. Towards the end of the period washing also increased and was observed almost twice as much as scratching. Scratching did not show a sharp increase but was still observed fairly frequently.

Locomotion

During the first fourteen days of the juvenile period, locomotor activity was very high. Walking remained at the same level of performance as in the socialization period and decreased later in the juvenile period.
However, the high-intensity locomotor patterns showed a considerable increase: running, jumping, dallying and turning were observed to reach a peak on the 37th and 45th postnatal day. The data tend to support the suggestion already made in respect of general rate of activity during the juvenile period.
At the end of the period, climbing became a favourite activity, notably in females.

Exploration

The amount of time spent on exploration remained very high, but did not increase any further. However, the pattern of exploratory activities changed. The exploration bouts, being very frequent but short-lasting at first, became less frequent but continued for longer periods of time, resulting in about equal total times.

Maintenance activities

During the juvenile period increasing time was spent on eating and drinking.

A characteristic of the juvenile period is a shift in behaviour performance. During the first fourteen days play behaviour is extremely frequent and animals behave much as in the preceding period. Suddenly the rate of overall performance decreases and performance becomes adult-like. The animals lose interest in each other and gradually spend more time on solitary activities such as grooming, eating and drinking. The decrease in general activity corresponds with the simultaneously developing differentiation between males and females, manifest in antagonistic behaviour patterns and in sexual activities.

I.3.6. The subadult period

General information

Two observation sessions were performed between postnatal days 60 and 90. Despite the paucity of quantitative observation some valid general statements about behaviour performance can still be made.
The period might best be characterized as one of stabilization. In comparison with the quantitative data gathered at the end of the juvenile period, quantitative records of days 75 and 90 did not differ to any considerable extent. Qualitatively, the performance of the subadults equals the performance of adult animals. Behaviour patterns are complete and abrupt changes in activity only rarely occur. Time spent on distinct elements increases because the elements are performed in an elaborate way; some specific patterns e.g. grooming and exploration, are continued for longer periods of time. In interactions the behaviour elements of the partners appear to be adjusted to each other. Moreover, the integration of distinct behaviour elements into normal adult sequences continues. Registration becomes somewhat easier since various patterns can be rapidly recognized and distinguished. The animals do not change their activities as often and as unpredictable as they did in earlier periods.
In our study, a female from one of the litters gave birth to her first offspring within the subadult period, on day 85. Since gestation time in rats is $\pm$ 21 days, this implies that sexual maturity of male rats was indeed reached on about the 60th postnatal day. During the observation session on day 90 the lactating mother

spent the whole time inside the nest, crouched over the pups.
In another litter a dramatic change was observed in antagonistic fighting behaviour during the observation session on the 90th day. For the very first time in the study, two male rats fought seriously and vigorously. Very suddenly a seemingly playful fight developed into a serious fight. Qualitatively speaking, the fighting behaviour instantly took on the characteristics of severe aggression: both animals had their fur standing on end, teeth chattering was noticed and the two types of ultrasonic "aggressive" vocalizations (Sales, 1972) were emitted. A new behaviour element known as clinch was also observed. As a result of the serious fighting both males suddenly exhibited the characteristic "cautious" behaviour performance: locomotory, exploratory and investigatory movements became hesitating, and freezing occurred.
The other animals in the litter seemed very interested in the fighting pair and kept their attention directed upon the two antagonists. The two animals fought repeatedly for short periods within the 15 minute session. After the observation session both males were examined for wounds, and both were found to have open bleeding wounds at the back and around the belly region. Serious fighting at this age probably functions to establish a dominance hierarchy between the males. During the adult period an even more dramatic development of antagonistic encounters between males fighting for dominance, was observed (vide infra).

As already mentioned, this was the first serious fight observed during the study even including casual observation of the litters between the official observation sessions. Serious fighting seemed to develop gradually out of harmless fighting and was clearly not an immediate consequence of reaching sexual maturity. Seward (1945) and Ewer (1972) have also reached the same conclusion. Seward observed a transition from playful fighting to serious fighting as early as the 45th postnatal day. This discrepancy in the age of onset of serious fighting may be due to a difference in environmental or rearing conditions. From our own observations on rats reared in isolation, it became clear that young rat pups are able to fight like adult rats as early as the 30th postnatal day. The fighting behaviour exhibited all the externally observable signs characteristic of a highly aggressive motivational state (chapter 2). Calhoun (1962) observed two animals of 35 days old, which having both walked into the same trap, began fighting fiercely upon the approach of the observer. In a study on pain-elicited aggression,

Hutchinson et al. (1965) report serious fighting in pairs of animals during the juvenile period following the administration of electric shocks.
According to Calhoun (1962) and Ewer (1972), subadult animals living under natural conditions, lose their immunity to adult aggression after reaching sexual maturity. From that time on they are liable to very aggressive approaches from adult rats. Calhoun observed a mother rat chasing subadults aged between 60 and 85 days, away from the nesting place. The chasing behaviour of the mother was quite unfriendly. During the same age period the interactions between the adult and the subadult males became highly aggressive. The aggressive behaviour of the adults clearly served to force the subadults to disperse and establish their own territory elsewhere. The same phenomenon was reported by Ewer: subadult rats (rattus rattus) were observed to emigrate as a result of hostile encounters with adults or even without any observable external cause detectable. They had to establish their own territory elsewhere. The observations of Calhoun and Ewer seem to be well in accordance with the phenomena we observed in the seminatural environment, but since no adult rats were present at this stage in our study, no statements about the subadult-adult interactions can be made. Continued observation of one of the litters over a period of about 10 months, did however, produce results of interest in this respect (see I.4.6.). The bouts of serious fighting between the males, observed on day 90 in one litter and soon thereafter in the other litters, may be interpreted as being consistent with the dispersion phenomenon, and to reflect attempts to gain a territory. Because of the impossibility of flight, retreat or continued avoidance, the animals are obliged to develop a temporary dominance hierarchy in the restricted environment of our study.

Social behaviour

Quantitative data indicate that the total amount of time spent on social activities stabilizes at about 12% of the total observation time. Most of this time is spent on agonistic activities, all of which were not serious with the one exception of the fight between two animals on day 90, already mentioned. The relatively high incidence of such elements as keeping off (in a lying position) and boxing on day 90 is to be ascribed to the two fighting animals. These two rats

were also responsible for the observed clinching behaviour: they lay motionless twisted around each other. In this position rats will eventually bite their partner, resulting in fighting bouts. Of the elements in the social exploratory category, the total time spent on anogenital inspection still increases slightly. Subadult males are responsible for almost the total time recorded for this element. The scores achieved on the other social investigatory patterns did not differ considerably from the results found on the 60th postnatal day.
Grooming the partner did increase in comparison with scores yielded during the juvenile period. Social grooming was performed both by males and females, although males spent twice as much time on this activity than females did at the ages of 75 and 90 days. Whether this activity is a precursor of aggressive behaviour, or correlates with it in some particular way, is not clear from our results. In a study on social behaviour with Wistar albino rats, Timmermans (1977) encountered an opposite result: female albino rats spent more time on social grooming than male rats.
The scores gathered for mounting behaviour show a rather freakish pattern. Mounting was very high on postnatal day 75 and decreased to a very low level on day 90. The sharp decay may partly be attributed to the fact that on day 90 most of the females were pregnant. On both observation days a number of mounting attempts were of a homosexual nature. Males were almost exclusively responsible for all the recorded mounting behaviour.

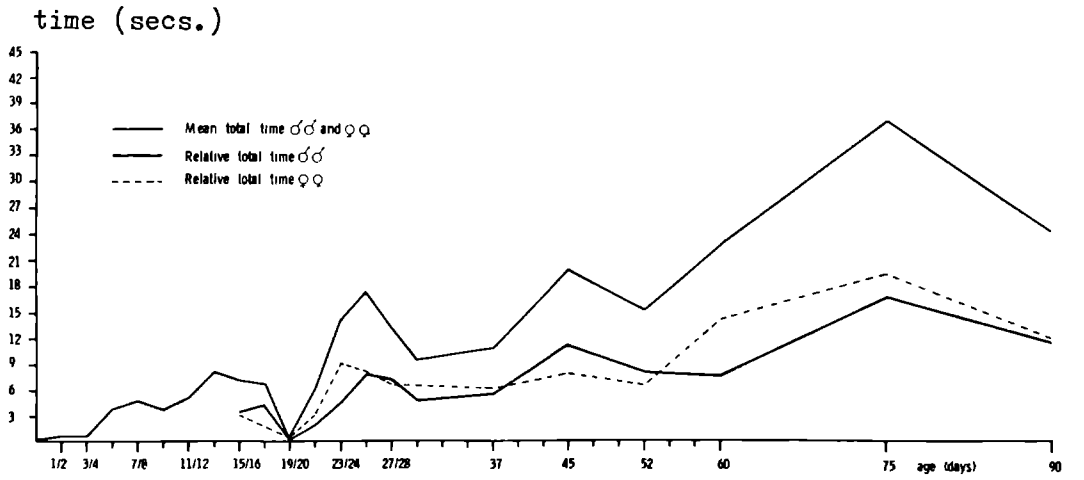


fig. 21. Scratch. Total time spent on scratching at various days of age.

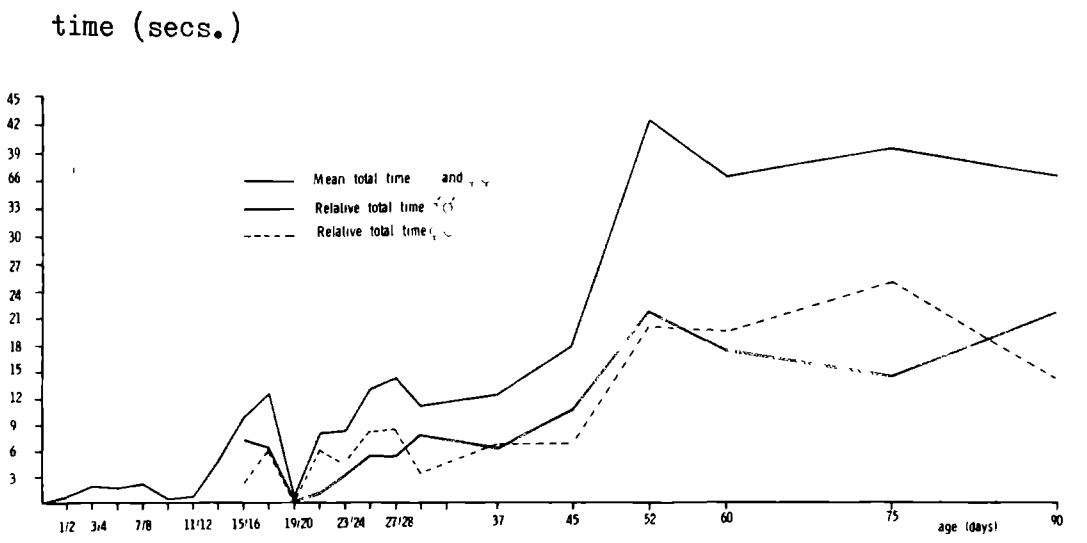


fig. 22. Wash. Total time spent on washing at various days of age.

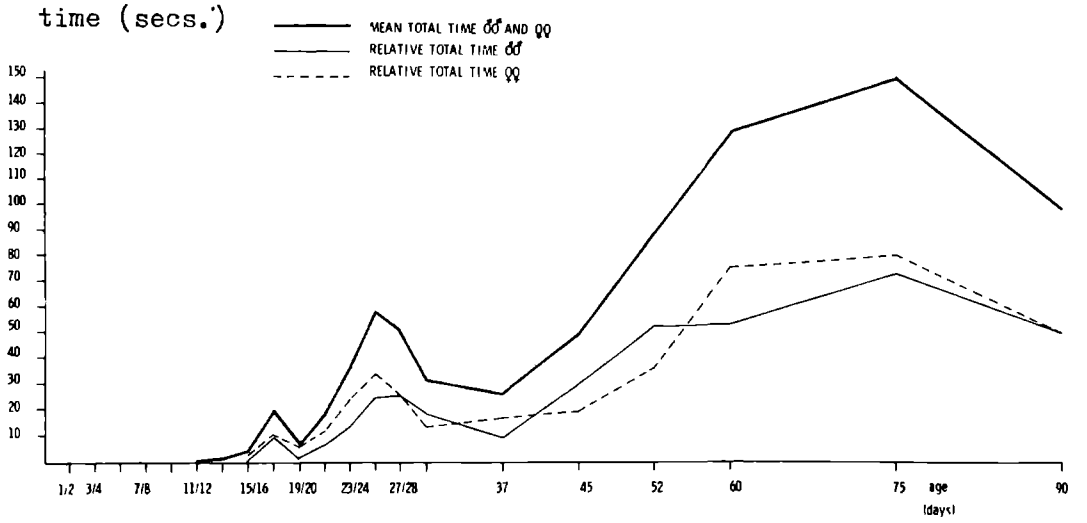


fig. 23. Groom. Total time spent on grooming at various days of age.

The bond between anogenital inspection and mounting had become obvious at this stage.

Comfort behaviour

As may be seen in fig. 21, 22 and 23, the three distinguishable activities involved in cleaning, viz. scratching, washing and grooming, were performed very often. Grooming especially showed an increase and became a favourite, frequently observed pattern of activity. In adult rats washing and grooming occur with very great frequency as any student of rat behaviour may confirm. The time spent on washing, scratching and grooming showed no considerable variations beyond the 60th postnatal day, whether taken together or analyzed separately. From the figures it may also be seen that throughout development, males and females do not differ with respect to the time spent on self-cleaning behaviour.

Locomotion

The frantic running and rushing locomotory patterns as well as the playful patterns dally and turn, have waned to a low level of performance. These elements, so characteristic at earlier stages,were only occasionally seen in subadult rats. Walking was observed fairly often and showed no further increase or decrease. Climbing remained a favourite activity in the subadult period. Analysis of observation scores indicated that the females preferred to climb. Between 70 and 80% of all climbing observed after the age of 30 days was performed by female animals.

Exploration

As is well known to any student of adult rats, exploration is by far the favourite activity of the animals. This statement may also be extended to subadult rats. Subadult rats perform exploratory behaviour in the same way as adult rats: they sniff at anything in the environment and these sniffing bouts have an increasing mean duration time with increasing age.

Other activities which took an increasing amount of time were such maintenance activities as eating and drinking. The increase of these solitary activities may indicate that in the subadult period rats begin to lose interest in each other and spend more time alone.
The total amount of time recorded for the element rest must be attributed to the lactating female who remained inside the nest throughout the 15 minute observation period. She was never disturbed by any of her littermates.

The subadult period is thus a phase of decreased level of activity in general, and of social activity in particular. The animals resemble adults in all respects. At the end of the period harmless agonistic male-male interactions are suddenly replaced by hostile encounters. This finding seemed so important, that we decided to extend study of the development of agonistic behaviour beyond the age of 90 days.

I.3.7. Adulthood (90 days)

General information

Non-systematic observations of the four litters were continued beyond the time originally set for the investigation. The development of that litter in which severe fighting had occurred on observation day 90 followed up until the animals had reached an age of about 10 months. The development of the other three litters was under observation for 6½ months. Two of the litters were left undisturbed: animals were allowed to breed and no limits were set to the total number of rats in the environment. In the case of the remaining two litters, all newborn rats were removed from the nests. The results of the continued observation were very interesting.
Following the 90th day, aggressive behaviour between males soon became apparent, even in those litters in which serious fighting had not previously emerged. Within every litter fighting clearly led to the formation of a dominance hierarchy, one male rat becoming dominant and the other two submissive. The establishment of the hierarchy could readily be deduced from signs of wounds, together with the

active avoidance and flight behaviour of the submissive males. The submissive males also showed a decrease in body weight. No evidence could be found with respect to a possible unidimensionality of dominance. On the contrary, the dominant male did not control the feeding place or the drinking tube, and was tolerant of the other males eating and drinking at his side. Furthermore, he was not exclusively responsible for the care of the offspring. The other two males were also observed to chase and mount the females. According to Baenninger (1966) rats reared in groups begin to develop a dominance hierarchy as soon as they have reached the age of 21 days. Baenninger found that the hierarchies remained stable throughout development until the animals were 4 months old, at which time the experiment was terminated. Careful scruting of our data, in respect of dominance among the adult males, did not however, reveal any correspondence with Baenninger's results. Our developmental data did not furnish any predictions about the formation of the hierarchy observed in adult males.

Hostile interaction between females did not occur. All females employed in the study became pregnant and delivered the first litter before they had reached the age of 4½ months. In the litter observed for 10 months, one female died during the process of parturition of her first offspring; she was 100 days old. In the litter breeding was not restricted and could be followed accurately. Only one of the two remaining females did breed succesfully and took care of her offspring. She was the only one who repeatedly built a nest and nursed newborn young. The offspring of the other female was scattered around the cage and was eaten by the adults. Occasionally the "good" mother retrieved and nursed pups born of the other female. The other unrestricted litter has not been observed on this phenomenon. However, Steiniger (1950) also reports that among wild rats inhabiting a confined area (64 m), only one female bred succesfully. The hostile encounters between males became gradually more severe. By the time the animals had reached an age of about 6 months, the outcome of fighting had become lethal. The dominant animal successively killed his brother and became the only surviving male. This phenomenon was observed in all four litters under study, and was therefore apparently unrelated to population density. It may be concluded that by the age of about 6 months territorial aggression reaches its peak. According to the observa-

tions of Calhoun (1962) and Steiniger (1950), individual territories are common among wild rats. In the natural habitat the opportunities for avoidance and flight result in dispersion at an earlier age, and thus prevent territorial aggression from becoming lethal. Furthermore the adult animals often find alternative pathways to the feeding place and arrange their feeding times so as to avoid confrontation with dominant rats (Calhoun, 1962).
The litter which was under observation for 10 months provided an even more dramatic example of territorial aggression. The adult male fiercely attacked the young male rats as soon as they had reached an age of between $3\frac{1}{2}$ and 4 months. These attacks led, without exception, to the successive deaths of all the young adult males. Often he would selectively pursue on one of the young for as long as two days. During these fighting bouts the adult himself sometimes became wounded. By the time the study had to be terminated, a total of eight young males had been killed by the "father". The general applicability of this finding would be premature, because in the other litters observation was terminated earlier. Timmermans (1977) however, observed exactly the same phenomenon in wild norway rats, Wistar albino rats and Tryon Maze Dull S3 rats inhabiting a seminatural environment of about 15 m^2. Timmermans found great differences between individuals and strains in respect of effective chasing and killing. In general Wistar albino rats were less effective than animals of other strains.

I.4. DISCUSSION

A study such as the one here presented, tends by its very nature, to raise more questions than answers, and it is perhaps precisely in this consequence that its major advantage is to be found. A preliminary descriptive study of behaviour development can be of great heuristic value in discovering the right questions to be asked. Furthermore, the state of an animal at a given point in its lifetime, may prove to be a crucial variable in well controlled experiments. It is also possible to study in detail particular behaviours which one wishes to understand. We feel that this study has suggested certain developmental trends about various categories of behaviour during the course from birth to adulthood.

The method employed has been a relatively simple one: direct observation of ongoing behaviour. Quantitative observation was based upon a list of descriptive behaviour elements. It should be clear that the use of ethograms in describing development has some important short-comings. First of all, it appeared to be too rigid: as already reported, during some stages of development, behaviour patterns were performed in an incomplete or "abbreviated" fashion. Yet the elements were still scored according to the description appropriate to the behaviour patterns of adults. The development and gradual completion of distinct patterns or postures, per se, cannot be included in an ethogram unless it be extended to a rather unmanageable list. Qualitative observation may be of great help here, and quantitative records certainly have to be supplemented by qualitative comment.

The second disadvantage concerns the discontinuity implicit in using an ethogram. The continuous stream of behaviour performance becomes artificially fragmented by application of structured observation. As long as behaviour elements can be distinguished fairly easily, and changes in behaviour occur in a rather predictable way, continuous observation, using a list, does not reduce the validity of statements based upon it. But in rat development some phases of ongoing behaviour become so kaleidoscopic in nature as to make continuous observation by the human eye a rather doubtful method. Inevitably the resulting records contain severe biases. Detailed frame by frame analysis of high-speed cinematographic records may form a useful aid in trying to disentangle the complete network of patterns and postures. It is felt that refining the observation technique, may provide valuable insight into the process by which complex adult patterns are gradually built up out of relatively simple ones. Moreover, the method of observation must be improved in order to be able to refine analysis of behaviour. In order to be able to make correlations between behavioural and neurological findings, developments in analysis of behaviour will have to keep pace with research developments at the neuroanatomical, neurophysiological and neurobiochemical levels.

The ethological approach is a time-consuming one that provides an enormous quantity of data. In the course of the present study we collected as many as 453,600 seperate items. A major difficulty is that of bringing order into such a mass of data. This study was designed to indicate trends in development and that is exactly what has been done. In order to make statements more "hard" and of increased validity, further selective investigation must be carried out. By focusing on certain aspects exclusively, those areas which have received too little attention in our study, may be researched in detail. The present study may also be helpful in indicating what should be included or excluded from observation with respect to the investigation of specific problems.

The course of behaviour development in the rat from birth to adulthood has been divided into distinct periods. From an inductive point of view such a division seems valid since major changes in social behaviour do indeed occur, and it is also a convenient help in describing the continuous process of development. The distinction has however its subjective and arbitrary aspects, with which one may easily feel out of sympathy. I have endeavoured however, to take into account as many characters as possible.

A final point to discuss, which has not been referred to so far, is the variation existing within development. Variations between animals or between litters were often considerable, yet since emphasis was on the development per se, and not on individual types of rats, the lumping of data seemed justified in describing trends This in no way indicates that any rat developed exactly according to the pattern described. Variations were sometimes too large to permit statistical analysis. For one thing, the seminatural environment in which the animals lived, may be responsible for the large individual variations observed. Furthermore, it may well be that there are different types of rats which during the course of their development tend to differentiate. Far more data would have been needed to trace such a differentiation within distinct types. Since there is an almost total lack of any information on the existence of individual types of rats, such a study would certainly be worthwhile.

It may be concluded from this study that social behaviour in rats develops in a regulated manner. The development of social behaviour is not an independent

process but is closely correlated with the development of other types of behaviour. The development of the central nervous system also seems to proceed in a regulated fashion, as can be concluded from the publications on neurological development. In future, the integrated study of behaviour development in all its aspects, and of the simultaneous development of structures mediating behaviour should be undertaken with great rigor in order to arrive at a comprehensive, holistic view of the social behaviour development of the rat.

A distinction may be made between the descriptive inductive and the experimental deductive approaches in scientific research. The developmental study which was reported in chapter I, should be characterized as mainly descriptive. Out of the preliminary descriptive study questions are easily generated as to what aspects in social behaviour development are worth being answered and which problems can be attacked in more restricted experimental research settings.
One of the interesting objects of study in the development of social behaviour is the question to what extent this development is dependent on growing up in a social environment. The experimental investigations to be reported in chapter II were designed to unravel the impact of social environment. The studies emerged from the findings of the descriptive study and intended to elucidate distinct processes during social behaviour development of the rat by focusing them in greater detail.

Age (days)

	1/2	3/4	5/6	7/8	9/10	11/12	13/14	15/16	17/18	19/20	21/22
Huddling	15700	17269	16299	16768	18139	18368	16319	18383	13028	18973	11957
Push past	2359	2259	3011	2426	1950	1841	1449	712	1327	432	596
Crawl across	1292	898	1042	1093	584	643	568	370	460	180	176
Righting response	1067	212	76	100	112	45	9	2	2		
Rest	387	40	68				8	2	103		
Crawl	382	278	323	300	138	70	76	18	6	4	2
Exploration	232	369	293	372	368	283	2535	1408	4764	1567	5914
Fall down	46	40	31	57	24	27	26	6	4		1
Sleep	45	21	66	50				3			
Convulsions	44	75	107	114	83	92	34	35	5	4	2
Scratch	22	19	105	118	93	134	190	174	169	10	147
Wash	17	51	48	57	15	28	116	237	300	22	187
Yawn	7	62	113	112	79	47	9	21	10	34	14
Stretch		3	5	19	11	18	8	17	2	6	
Drink reflex		2	13								
Shake		2		14	4	2	13	2	11	6	9
Walk						2	193	59	264	35	260
Eat							15	6	182	98	204
Groom							20	110	467	144	440
Pull							8	22	4		3
Climb								2	44	11	139
Investigate								8	166	23	507
Social grooming								3	65	1	86
Fight									16		199
Keep off									56		28
Keep down									30		63
Follow									6		11
Standing attention									14		26
Retreat									7		40
Strike									7		14
Dig									27	46	23
Dally									31	4	67
Turn									6		20
Sit									1		17
Gnaw									8		125
Drink									7		84
Throw up									1		
Kick											33
Squirm											18
Push over											4
Oral inspection											7
Sideways defense											13
Nosing											16
Upright posture											11
Lunge											48
Box											46
Mount											4
Jump											17
Grub											8
Pick up											4
Run											10
Hop											
Flee											
Drag											
Anogenital inspection											
Paw											
Shrink back											
Clinch											

Table 1. Total time spent on different activities at different ages. Number of subjects is 24. Unit time per subject is 900 seconds.

	Age (days)									
	23/24	25/26	27/28	29/30	37	45	52	60	75	90
Huddling	5570	4650	2991	1524	2	94	549		12	140
Push	571	124	157	279	140	68	45	24	55	79
Crawl over	145	34	22	28			31		8	1
Righting response										
Rest	13	56	337	210	70	395	1694	13	1382	889
Crawl		2								
Exploration	7712	8814	9667	11360	10177	8655	10119	8416	9053	9120
Fall down				2	2					2
Sleep	2			3				5		
Convulsions										
Scratch	334	414	358	238	284	486	377	547	894	585
Wash	196	332	313	285	301	432	1012	887	958	884
Yawn	1				4	10	4		20	8
Stretch	3		3		4	18	8	7	15	6
Drink reflex										
Shake	6	22	22	17	51	69	70	117	56	61
Walk	381	509	484	735	666	721	434	533	604	615
Eat	2199	1673	1093	1161	1868	2683	1303	2278	1646	2590
Groom	869	1393	1094	764	626	1163	2149	3095	3686	2374
Pull	18	9	4	23	41	13	3	55	1	
Climb	102	131	188	208	652	429	438	1138	420	712
Investigate	310	462	470	606	508	633	318	664	363	700
Social grooming	110	510	412	147	68	282	136	95	205	315
Fight	445	529	1160	785	1209	1314	362	457	172	232
Keep off	89	67	62	148	188	563	215	290	49	233
Keep down	226	214	281	447	747	763	290	387	154	263
Follow	24	34	51	86	65	39	27	35	28	29
Standing attention	44	42	44	77	173	60	68	232	64	65
Retreat	22	30	50	101	132	39	61	72	32	34
Strike	140	132	287	316	361	553	160	196	56	157
Dig	63	98	126	62	30	140	50	120	4	20
Dally	189	154	165	246	97	264	41	95	14	8
Turn	14	17	26	27	62	27	18	24	3	13
Sit	38	166	11	177	16	10	24	81	242	64
Gnaw	67	41	14	165	6	21	86	35		27
Drink	1300	251	682	474	687	624	518	633	640	587
Throw up		2	9	8	7	18	27	72	10	11
Kick	58	146	255	172	211	268	253	210	183	180
Squirm	141	101	183	165	516	247	55	101	39	53
Push over	1	5	7	13	525	17	36	6	1	5
Oral inspection	4		7		16	13	11	5	14	7
Sideways defense	29	39	89	74	180	60	68	78	76	68
Nosing	4	6	2	8	2	2	2	6	10	
Upright posture	10	9	20	21	41	7	17	52	7	2
Lunge	37	80	59	80	192	39	9	26	4	17
Boxing	10	48	72	20	64	42	84	78	10	136
Mount	9	14	55	81	68	65	104	65	121	24
Jump	54	89	126	215	253	122	91	198	43	80
Grub										2
Pick up	4									
Run	27	45	127	23	204	89	92	7	38	14
Hopping	4	6	12	3	24	1	10	20	18	32
Flee			2				1			
Drag				4						
Anogenital insp.	5	9	1	12	42	42	130	145	189	146
Pawing					4					
Shrink back		1			14				1	
Clinch										10

Table 1. Total time spent on different activities at different ages. Number of subjects is 24. Unit time per subject is 900 seconds.

II. ONTOGENETIC ASPECTS OF ISOLATED VERSUS GROUPED REARING

II.1. INTRODUCTION

"The child is the father of the man" is a statement which emphasizes the importance of early experiences and development during individual life histories for the behaviour of adult organisms. Over the last two or three decades many studies in animal psychology have been devoted to the effects of early experience or early stimulation upon adult behaviour. These studies were mainly inspired by psychoanalytic theory and by the suggestion that early experience might influence the development of intelligence. Research into the effects of different experiences during various periods of ontogeny was primarily based upon the assumption that during a so called critical period, certain experiences would produce specific effects in adult life. The concept of a "critical period", stemming from embryology, has been subject to much criticism. Denenberg (1964, 1968) for instance, considers the term to be practically useless for behavioural studies because of the implicit connotation of irreversibility of effect, which in fact does not exist. Beside this the critical periods of behavioural development cannot be limited within exact boundaries of time. But, above all, it seems that there are almost as many "critical periods" as there are possible combinations between independent variables (experiences) and dependent variables (behavioural parameters). Students of behavioural development now tend to prefer the term "sensitive period" as more appropriate: a given period is optimal for being liable to certain forms of stimulation as contrasted with suboptimal periods. The term sensitive period is also preferred because the connotation of irreversibility is not implicit in it.

In laboratory studies concerning the effects of early experiences in rats and mice three sensitive periods can be distinguished: a) the prenatal period, b) the postnatal, preweaning period, and c) the early postweaning period. With respect to the independent variables a distinction may be made between a) experiences of short duration involving rather intensive physical or mechanical stimulation, such as handling, shock, temperature or sound and b) experiences of longer duration involving fairly constant environmental manipulations, such as mother-young interaction,

mal- or undernutrition, enriched or impoverished environment or social isolation.

Many parameters, psychological or physiological, have been selected as the dependent variable in order to measure the effects of manipulations on adult behaviour early in the life histories of the animals. Levine (1969) stressed the importance of the choice of suitable responses as dependent variables: the kind of conclusions made are dependent on the nature of the situation in which the organism has to behave, and the quantifications often determine the qualitative aspects of the behaviour of the animal. The selection of a restricted laboratory setting in order to study certain separated aspects, should therefore be made with care. The situation chosen should be adequate for the selected aspects of behaviour. Beside this, the behaviour parameters selected should be representative of the aspects to be investigated. These remarks concerning the choice of the dependent variable do not hold exclusively for the study of behaviour development, but are of course of general applicability to animal behaviour studies.

II.2. SOCIAL ISOLATION

A technique widely used in animal developmental studies, consists of isolating the animals for a certain period during ontogeny and testing these animals later on in order to determine the effects isolation brought about. Originally it was a technique especially favoured by students who -stressing the importance of the nature side of the nature-nurture dichotomy- tried to convince their opponents that in spite of a lack of experiental learning, animals continue to develop certain behaviour patterns and postures. Later on, as the nature-nurture controversy waned, isolation as a technique used in animal studies, remained in vogue because of the rather consistent effects it produced. Several authors, working with a number of distinct animal species, repeatedly reported the deleterious effect that social isolation had on the development of social behaviour.

In particular, an increase in aggressive behaviour induced by a period of isolation was consistently found. Harlow et al. (1965) working with monkeys found them becoming hyperaggressive after a period of isolation. Moreover, normal social and sexual behaviour was severely disturbed. A sharp increase in aggressiveness was also found by Hull et al. (1973) in a study using guinea pigs as experimental subjects.

A number of students found hyperaggressivity resulting from social isolation in mice as well (Welch and Welch, 1969; Cairns and Nakelski, 1970, 1971; Banerjee, 1971; Harmatz et al., 1975).

The results of studies using rats as experimental animals are more controversial. In these investigations, dominance behaviour in restricted environments was often chosen as the parameter in studying effects of isolation on intraspecific aggressive behaviour. The choice was based on the implicit assumption that the test situations were suitable for eliciting aggressive behaviour from the animals. Aggression would then result in dominance behaviour. For instance, Ward and Gerall (1968) using a so called dominance tube as a test situation, found that isolated rats were dominant over socially reared rats. Weaning and time of onset of isolation took place rather early, at the age of 14 days. Howells and Kise (1974) were able to confirm this finding. In an underwater tube test, isolated subjects were dominant over their socially reared partners. However, if tested in a food dominance situation, socially reared animals turned out to be superior to isolated subjects. In this investigation animals were weaned at the age of 28 days and isolated at the age of 55 days. Connor and Gregor (1973), weaning their subjects at 21 days and isolating them for 56 days beginning at the age of 45 days, report that in a lever press situation significantly more aggressive, subordinate and social contact behaviour was to be found in isolated animals as compared to group-reared ones. Unfamiliarity with the test situation on the part of one animal in an isolated-isolated pair, led to less aggressive behaviour due to the interference of extensive explorative behaviour of that animal. Masur and Struffaldi (1974), using a dyadic worker-parasite bar press situation, found that in the isolated-isolated pairs social contact behaviour and aggressive behaviour initially prevented bar pressing from being performed at the same level as in the grouped-grouped pairs. In the grouped-isolated pairs the grouped animals always became the workers. Isolated animals tended to be more interested in chasing and fighting their partners, than in bar pressing and drinking.

Rearing in isolation also has an effect on interspecific aggression: isolated rats show an increase in aggressivity towards non-conspecifics such as frogs or mice. Johnson et al. (1970) found that socially experienced rats react less aggressively on the presentation of a frog than rats reared in isolation. The social group con-

tained a lower percentage of killer rats and their latency times for attack were longer. In another study the same authors (1972) were able to replicate these results. Myers (1969), however, could not demonstrate a difference in mouse-killing behaviour between isolated animals and group-reared ones. After a three week period of isolation, Valzelli and Garattini (1972) found a rather low percentage of killer rats in a muricide test. The percentage of killers did increase with prolonged isolation time. Lorenz (1972) showed an effect of age of isolation on the muricide parameter. Animals which had been isolated at 22 days of age, killed significantly more often than animals which were weaned at the age of 17 days and isolated thereafter.

Not all studies, however, were succesful in demonstrating an increase in intraspecific aggression as a result of rearing in isolation. Rosen (1961), for instance, using a water competition situation, could not find a significant difference in dominance behaviour between isolated and group-reared rats. Dolger (1955), using a water competition situation as test environment, found rats raised in a social environment to be dominant over rats raised in isolation. Also Hutchinson et al. (1965) observed that group-reared rats fought more in a foot-shock experimental situation, than rats reared in isolation. Moreover, 't Hart (1974) observed less aggressive behaviour in isolated animals in comparison with group-reared ones; unfortunately he does not give any details concerning the methodology he used. Korn and Moyer (1968) did not observe any aggression between pairs of isolated animals in a free test situation, but their test period lasted for only four minutes. However, in this case the isolation of the animals commenced only after they had reached adulthood.

This short review reveals the enormous extent of variations in the methodology used in social isolation studies. It is precisely this lack of standardization which makes it so difficult to give a unified interpretation of the seemingly contradictory results found in these studies. Firstly, there are large variations in the means employed for producing isolation in the animals. Age of weaning, age of onset of isolation and duration of the period of isolation often differ substantially in the various investigations mentioned. The test environments used to elicit aggressic also show remarkable differences, e.g. water competition, dominance tube, open field and shock induced aggression. Some investigators tested the animals in pairs

while others exposed them to a group. Exposure times in the particular studies showed large variations too. Furthermore, different rat strains were used. But most important of all, there exist substantial variations in the parameters used to assess isolation-induced aggression: latency of onset of first attack, number of fighting bouts, total time spent on fighting and frequency scores on a small number of behaviour elements.

The aggressive behaviour of the isolated animals under study has been almost always described very poorly. Moreover in most studies the role and behaviour of the test partner(s) has not been taken into account although it should be clear that the actions or reactions of these are extremely important. It is possible that a more detailed and accurate description of the total behaviour of the animals could be an important key to the solution of the discrepancies in the results found.

Isolation does not only affect aggressive behaviour in rats, it produces effects on other behavioural aspects, both social and non-social as well. An increase in gregariousness or social seeking behaviour following a period of isolated rearing has been repeatedly reported (Latané et al., 1970; Latané et al., 1972; Connor and Gregor, 1973; Masur and Struffaldi, 1974). The opposite effect was found in some other studies (Ashida, 1964; Singh and Maki, 1968).

Sexual behaviour also seems to be severely disturbed. A number of investigators report a complete lack, or a substantial impairment of sexual behaviour in adult rats which had been reared in social isolation since birth or weaning (Folman and Drori, 1965; Gerall et al., 1967; Hard and Larsson, 1968; Gruendell and Arnold, 1969, 1974; Diener, 1970; Allan and Boice, 1971; Duffy and Hendricks, 1973; Spevak et al., 1973; Wilhelmsson and Larsson, 1973).

Results on the effects of isolation upon general activity measures are rather controversial (Koch and Arnold, 1972; Archer, 1969; Huntley and Newton, 1972), and this again reflects the lack of uniform parameters for measuring activity in these studies.

Emotionality was consistently found to be higher in isolated animals (Dolger, 1955; Koch and Arnold, 1972; Korn and Moyer, 1968; Taylor and Constanzo, 1975).

Isolation was shown to induce neuroanatomical (Essman, 1971), neurobiochemical and neurophysiological changes too (Valzelli, 1973; Hatch et al., 1965). Because of the manifold changes isolation brings about, the latter two authors use the term "isolation syndrome" in describing the entire complex of consequences following isolated rearing.

The investigations which will be presented in the next paragraphs have been performed in order to study with the greatest possible accuracy exactly what changes isolated rearing induces at the behavioural level in comparison with grouped rearing. It was felt that the ethological method of observation, focusing on total behavioural output of the animals, would be the most suitable method for answering, in sufficient detail, the various relevant questions. An exact morphological description of behaviour could perhaps throw some light on the contradictory results reported so far. Since the method employed permitted analysis of the behaviour of the test partner, the role of the partners could also be studied in detail. Moreover, the experiments we designed so as to permit in-depth study of ontogenetical aspects of isolated and grouped rearing which have not attracted much attention in earlier studies.

II.3. MATERIAL AND METHODS

II.3.1. Animals

In the series of investigations a total of 300 male rats were used. All animals came from a breeding stock of Tryon's maze dull (TMD) strain, which is maintained in the Psychological Laboratory of the Catholic University of Nijmegen, the Netherlands.

II.3.2. Housing

All animals were weaned at 23 days of age and then randomly assigned to one of two rearing conditions: a) isolated rearing and b) grouped rearing. The isolated animals were housed individually in macrolon cages, measuring 35x24x16 cm. The grouped animals were housed in groups of four, also in macrolon cages, measuring 56x34x20 cm. Since all animals were kept under equal conditions in the same room, isolation was not total. It was possible for the isolated rats to receive visual, auditory and olfactory cues from other animals. The cage floors were covered with sawdust and were cleaned weekly. Water and food were available as lib. Animals were kept on a reversed 12 hr. day-night cycle, the dark part of the cycle starting at 10 a.m. The room was air-conditioned and temperature was set at $23^{o}C$.

II.3.3. Procedure

After a variable period of either isolated rearing or grouped rearing the animals were tested in pairs, according to the following testconditions:

a) I-I confrontations — These animals were isolated immediately after weaning and tested against a partner, which had been isolated for the same period.

b) I-G confrontations — These animals were isolated immediately after weaning and tested against a partner, which had been raised in a group for the same period.

c) G-I confrontations — These animals had been raised in a group after weaning and were tested against a partner, which had been raised in isolation for the same period.

d) G-G(U) confrontations — These animals had been raised in a group after weaning and were tested against an unfamiliar partner, which had been raised in another group for the same period.

e) G-G(F) confrontations — These animals had been raised in a group after weaning and were tested against a partner from the same group.

Testing took place after the animals reached an age of 30 days, of 60 days, of 90 days, of 120 days, of 150 days or 180 days. Each animal was tested only once, to avoid confounding of the effects of repeated testing and the effect of age. In total 30 groups (5 testconditions x 6 age-levels) were used, each group consisting of 10 animals.

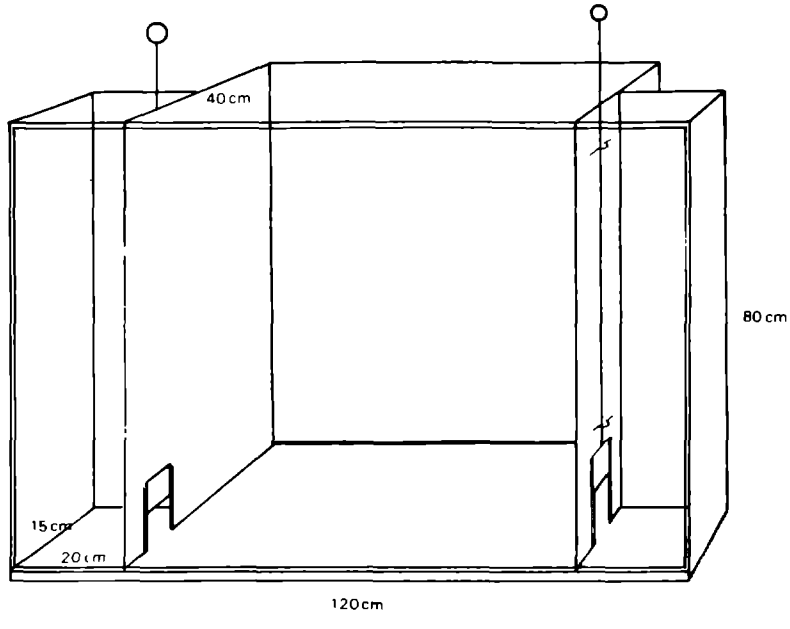


Fig. 24. The observation cage used to observe the behaviour of the rats.

The rats were tested in pairs in an observation cage, measuring 80x40x75 cm. (fig. 24). The cage had a front wall made of glass, permitting a good view into it. The back wall and the two side walls were of sheet metal. In each of the two side walls a doorway of 6x6 cm. was made, which could be opened and closed by sliding doors. The doorways gave entrance to a compartment, measuring 20x17x75 cm. attached to the side walls. The front walls of the small compartment were made of glass too. A drinking tube and a food hopper were attached to each of the two small side walls of the observation cage. The floor of the test cage was made of wood and covered with sawdust. The floor of the testcage could be separated from the rest of the cage. The observation cage has been designed by Timmermans (1977) as a standard test situation for observation of dyadic rat confrontations.

During the last three days prior to the day of the dyadic test the animals were given the opportunity to explore the observation cage. On each of these three days each animal of a pair stayed alone in the cage for 2 hours, in order to become acquainted with the test environment. Each test-pair received their own floor covered with fresh sawdust at the beginning of the exploration period. On the test-day the pair was placed in the observation cage on the same wooden floor and sawdust upon which they had already been placed during the three days exploration sessions. The sliding doors to the side compartment remained open during the exploration sessions so that the animals had the opportunity to explore the whole test environment. Exploration always took place during the dark part of the reversed day-night cycle. During the exploration sessions and the test sessions, water and food were available ad lib.

On the day of testing the pairs were transported to the observation room. Each animal from a test pair was placed in one of the small compartments and the entrances from the compartments to the observation cage closed. After five minutes the doors were opened, giving the animals the opportunity to enter the observation cage and to meet each other. From that moment on, the behaviour of the two animals was recorded on videotapes for 15 minutes. During the test session the doorways remained open. The room used for the experiment was empty except for the observation cage, a camera used for recording and two microphones used to pick up sounds produced by the animals. The observation cage was illuminated by a light-unit, containing four

15W red lamps behind an opaque glass front. The light-unit was suspended from the ceiling just above the box. All observational recording took place at the beginning of the dark part of the day-night cycle. No more than three dyadic confrontations were recorded on the same day.

II.3.4. Material

The camera used was a Tivicon ITC CTC 6000, containing a Canon motorized zoom lens TV 6x16. The camera was highly sensitive, permitting excellent recording under the dim red light conditions existing in the experimental room. In an adjacent registration room the experimenter, while watching the recording of the test session on a Shibacon video monitor, was able to manipulate the camera and motorized zoom lens by means of a Philips manual automatic keyboard. Audible sounds produced by the animals were recorded on one channel of the two-channel audio receiver unit of the IVC 711 videorecorder. A microphone type Sennheiser MKH 405 was used for reception of these sounds.
Ultrasonic noises were converted into audible sounds and recorded on one channel of a stereo two-channel Philips PRO 12 taperecorder. The microphone used to pick up the ultrasounds was a Bruell and Kjaer 4135 field condenser microphone. The receiver used for conversion of the ultrasonic signals into audible sounds was a self-made model and similar to the "bat-detector", described by Pye and Flinn (1964). The second audiochannels of both the videorecorder and taperecorder were used to register a repeated time signal which could be used to synchronize behaviour performed and sounds emitted, when the tapes were played back for analysis.

II.3.5. Analysis of behaviour

A list of 64 behaviour elements was used in the behaviour analysis. The list was partially derived from the one printed elsewhere (pages 7 to 15), but in this case was somewhat more extended and detailed. Since the emphasis was on studying aggressive behaviour, the number of elements in the antagonistic categories was increased. The extension was made partly due to the fact that a number of behaviour patterns did not show up in the first study whereas they did in this one. On the

other hand, in order to enable a more refined and detailed analysis, particular elements were added.
The list contained the floowing postures or patterns. A new element, not used before, will be defined. Descriptions of other elements were given earlier (pages 7 to 15).

SOCIAL BEHAVIOUR

Social exploration

a) attentive at distance:

Approach	Locomotory movement in the direction of the partner. Includes stretched approach.
Attend	Direction of head and/or body to the partner.
Follow	Locomotory movement directed to a partner which is moving away.

b) in physical contact:

Investigate	
Nose	
Oral inspection	
Anogenital inspection	
Crawl under	Animal crawls under the partner's body from the front or from the side. This element is usually accompanied or followed by anogenital sniffing.

Social contact behaviour

Social grooming	
Aggressive grooming	As in social grooming. The behaviour however is performed with great intensity.
Crawl across	
Touch	Touching the partner with one or both forelegs, irrespective of posture.
Take hold	Clasping the partner with both forelegs around the back, either from behind or from the side.

Hold fast	Keeping clasped to the partner for an extended period of time.
Dash	Running into the partner.

Sexual behaviour

Mount	
Present (passively)	Sitting with back lifted up, as a result of the partner's attempt at genital sniffing.

Antagonistic offensive activities

Push	
Push aside	Pushing the partner away with the forelegs. Often seen while the rats are eating or drinking.
Strike	
Pull	
Snap	A quick movement of the head, mouth open in the direction of the partner. Often alternated with strike.
Bend over	Placing both forelegs on the partner's back or belly and bending the head to the far side of the partner's body. Often resulting in bite.
Threat	Animal oriented broadside to the partner, head is kept low, ears extended and accompanied by piloerection. Often at some distance from the partner.
Impress	High intensity offensive sideways posture. Back is arched and body shortened. Distance to the partner is minimal. Head oriented to the partner.
Sideways attack	A behaviour pattern emerging out of threatening or impressing. Pushing against partner, while broadsided. Often bending the head under the lifted forepart of the body of the partner to the other side.

Lunge	
Fight	Includes clinging. Playful fighting not included.
Bite	Biting the partner's body. Often occurring in fighting or clinching bouts.
Push over and backward	
Keep down	
Chase	Running pursuit of a partner which tries to escape.

Antagonistic defensive activities

Evade	Sideways or upward movement of the head or body away from the partner.
Retreat	
Withdraw	Backward movement of the head or body away from the partner.
Flee	
Freezing	The animal sits, stands or lies down motionless. Often observed as a "cataleptic" posture following the submissive posture.
Keep off lying	
Squirm	
Fall sideways or backward	
Full submissive posture	Animal lies on his back, forced by the partner. Resulting from fighting or pushing over or backward.
Kick	
Sideways defensive posture	
Sitting defensive posture	Animal sitting on hindquarters, trying to keep the partner at a distance by extending forelegs and contacting the partner.
Shrink back	Frantic leap away from the partner.

Antagonistic ambivalent activities

Box	
Upright	Defense or attack in contact
Standing attention	Upright defense or attack without contact
Parry	Animal sitting on hindquarters oriented to the partner. Forelegs lifted up, no contact with the partner whatsoever.

NON-SOCIAL BEHAVIOUR

Exploration	
Stretched attention	Extension of the forelimbs, body fully stretched. Head also extended or lifted. Posture reflecting transition from sitting into locomotion.
Rocking	Animal sitting on four legs, head erect or lifted up, combined with rocking movements of the head from side to side.
Sit	
Rest	
Locomotion	
Dally	
Jump	
Dig	
Throw up	
Eat	
Drink	
Groom	Contains all cleaning activities, except licking wounds.
Licking wounds	Cleaning of fresh wounds, resulting from fights.
Tail rattle	Swaying movement of the tail. This element is seen (infrequently) in animals in a state of high agitation.

The behaviour of the animals was scored continuously from a monitor, on which the videotapes were played back. The shortest time-unit the experimenter was able to cover in transforming direct observation into written shorthand was one second. Thus for every second a behaviour element was jotted down in shorthand on a paper-graph recorder. By carefully comparing the records of both animals in a test pair, and by repeated replay of the videotapes, the records obtained could be corrected if necessary. Each animal yielded a behaviour record of 900 elements. The sequence of these 900 elements, thus collected for each animal, was punched on punching-cards for computerized analysis.

Sounds produced by the animals could be correlated with behaviour by playing back both videotapes and audiotapes synchronously.
Two measures were used for statistical analysis of the behaviour records of the animals in the distinct groups:

a) mean total time spent on a behaviour element
b) mean frequency of occurrence of a behaviour element, an index of initiating an element.

II.3.6. Statistics

Two analyses of variance were performed. In the first analysis the effects of rearing conditions of each of the animals in a pair and of the age of testing were examined. The groups used in the 2x2x6 design were the I-I, I-G, G-I and the G-G(U) animals. In the second analysis of variance the effects of familiarity and of unfamiliarity of the partner and the effect of isolation, per se, of a partner and of unfamiliarity of a partner, were examined. In the second analysis the G-I, G-G(F) and the G-G(U) animals were used in the design.

A) Three independent variables were examined with respect to their effects on the behaviour of the rats: 1) rearing condition of the test animal, 2) rearing condition of the partner, 3) age of testing.
The first factor had two levels: isolated versus grouped rearing. The second factor concerned the rearing condition of the partner and also had two levels: isolated versus grouped rearing.
Age was treated as the third factor, having six levels, i.e. 1 through 6 months.
Frequencies of occurrence and time spent were analysed for each behaviour element separately by performing an univariate three factorial (2x2x6) analysis of variance. All three factors were considered fixed. The expected mean squares are:

Source	df	Expected mean squares
Rearing test animal	1	$\sigma^2_\varepsilon + 120\ \sigma^2_\alpha$
Rearing partner	1	$\sigma^2_\varepsilon + 120\ \sigma^2_\rho$
Age	5	$\sigma^2_\varepsilon + 40\ \sigma^2_\gamma$
Rt x Rp	1	$\sigma^2_\varepsilon + 60\ \sigma^2_{\alpha\beta}$
Rt x Age	5	$\sigma^2_\varepsilon + 20\ \sigma^2_{\alpha\gamma}$
Rp x Age	5	$\sigma^2_\varepsilon + 20\ \sigma^2_{\beta\gamma}$
Rt x Rp x Age	5	$\sigma^2_\varepsilon + 20\ \sigma^2_{\alpha\beta\gamma}$
Within cell	216	σ^2_ε

All effects are tested against the within cell variances.

B) In a second analysis the effect of familiarity or unfamiliarity of a group-reared partner on the behaviour of a group-reared test animal was investigated. An attempt was also made to distinguish the effects of isolation, per se, of the partner and of unfamiliarity of the partner.

Again two dependent variables were analysed: the frequency of displaying a specific behaviour element and the total time spent on it. A univariate three factorial analysis of variance was performed, the factors being 1) rearing-isolated versus grouped rearing of the partner 2) familiarity-animals being familiar or unfamiliar with each other, and 3) age -1 through 6 months.

In the partially hierarchical design, the factor familiarity is nested under the factor rearing and the factor age is completely crossed. The rearing condition of the test animal has been held constant and has always been grouped rearing. All factors are considered fixed.

The expected mean squares are then:

Source	df	Expected mean squares
Rearing	1	$\sigma^2_\varepsilon + 120\ \sigma^2_\alpha$
Familiarity	1	$\sigma^2_\varepsilon + 60\ \sigma^2_\beta$
Age	5	$\sigma^2_\varepsilon + 40\ \sigma^2_\gamma$
Rearing age	5	$\sigma^2_\varepsilon + 20\ \sigma^2_{\alpha\gamma}$
Familiarity age	5	$\sigma^2_\varepsilon + 20\ \sigma^2_{\beta\gamma}$
Error	162	σ^2_ε

All effects are tested against the within cell variance. The effects of isolation and familiarity might be roughly compared by substracting the within cell variance from both the mean square for rearing and familiarity and dividing the remaining part of the mean square by 2.

II.4. RESULTS

II.4.1. Isolated versus grouped rearing; Test partner; Age.

The analysis of variance has been performed in order to study the main effects of rearing condition, test partner and age on the behaviour of the animals. In the first analysis of variance the I-I, I-G, G-I and the G-Gu animals were employed

in the design.

Means of the various behavioural frequencies and time spent on the particular elements, are tabulated for the distinct groups in tables 2 through 9 of the appendix. Figures of various elements and tables of the results of the analysis of variance are printed in the appendix on pages 142 to 151.Some of the elements were performed at a minimum level and did not permit reliable statistical analysis. In the case of a non-testable, yet substantial difference -e.g. the absence of an element in one group, while being performed by animals in another group- this difference was used in qualitatively comparing the distinct groups.

Social exploration

a) Attentive at distance

Approach. The analysis of variance revealed that isolated animals approached their partners less often than the group-reared animals did. Moreover, an isolated animal was not approached as often as a group-reared one. As animals grew older, the number of approaches decreased considerably. The isolated animals especially showed a sharp decrease with increasing age. At the age of 6 months however, the isolated animals equalled the group-reared ones in number of approaches due to a considerable increase in frequency of approaches.

Attend. Isolated animals attended to their partners more often than group-reared ones did. No significant effect was found resulting from the rearing condition of the partner. However, analysis of the significant rearing x partner interaction, showed that isolated rats attended to a group-reared partner much more often than to an isolated partner. There was a gradual over-all decline in attending with increasing age. The I-G animals showed a very sharp decrease, whereas attending in I-I and in G-Gu animals stayed about equal at all ages. By the age of 4 months the difference caused by distinct rearing conditions had disappeared.

Follow. A group-reared rat was followed more often than an isolated one. Isolated animals followed the group-reared partners very often, while only infrequently following an isolated one. The difference was limited to the first two test ages. By the age of 3 months, following had decreased to a low level in all groups.

Summary. With respect to the activities in the attentive-at-distance category, it can be concluded that isolated animals attended to their partners more often than group-reared animals did. However, they did not approach or follow their partners more often than group-reared animals did. Isolated animals confronted with an isolated partner showed a low level of the attentive-at-distance activities, whereas the confrontations between isolated and group-reared rats led to high frequencies of approaching, attending and following. The differences found were most prominent at the early test ages.

b) in physical contact

Investigate. No effect of rearing condition on frequency of social investigation was apparent. However, isolated animals spent far more time on investigating than group-reared animals. A group-reared animals was investigated more often than an isolated one, although there was no difference in total time. Frequency of occurrence and time spent increased slightly with increasing age. Isolated animals, confronted with group-reared partners, spent much time on social investigation.

Anogenital inspection. Highly significant effects were found for this activity. Isolated animals performed anogenital inspection less often than group-reared ones. Moreover, isolated animals were investigated at the anogenital region less often than group-reared rats. Most frequently anogenital inspection was observed in the G-Gu confrontations. Age also had an effect. Isolated animals, after a moderate initial frequency of performance, showed a decrease to a very low level with increasing age. Group-reared animals, however, showed a sharp increase in anogenital sniffing with increasing age. The differences thus found were larger at the later test ages.

The other behaviour elements in this category: nosing, oral inspection, crawl under, did not appear very frequently. Statistical analysis has therefore not been performed. However, the frequencies and total time measures found, indicate that group-reared animals are superior to isolated ones on all three elements. Moreover, isolated partners elicited less nosing, oral inspection, and crawl under than group-reared rats.

Summary. Isolated animals do not initiate social investigative behaviour more often than group-reared rats do. However, they do spend more time on this activity, which implies that they investigate their partners for a longer period of time. Anogenital inspection was rarely observed in isolated animals, but fairly often in group-reared ones. Differences in nosing, oral inspection and crawl under are in the same direction as the differences found for anogenital inspection. The frequencies of the last three elements were too low to permit statistical analysis.

Social contact behaviour

Touch. Animals reared in isolation touched their partners less often than group-reared ones did. At the age of 1 and 3 months the difference was considerable. In the I-I and G-Gu confrontations touching was less frequent at all ages. A gradual decline has been found with increasing age. The decrease in isolated animals was steeper than in group-reared animals.

Take hold. There was no significant effect of rearing condition on this activity. The rearing condition of the test partner did not have any effect either. Analysis of the significant rearing x partner interaction, revealed that for the first three test ages especially, take hold was frequent in the encounters between isolated and group-reared animals. A gradual decline with increasing age was found in all groups. Beyond the age of 4 months differences between the groups had disappeared.

Hold fast. An isolated animal was held on to for a longer continuous period than a group-reared one. It was notable that in the G-Gu confrontations holding on was observed very infrequently. Isolated animals held on to their isolated partners often during the first three stages. As the animals grew older the time spent on holding on decreased to a very low level in all groups.

The frequencies found for other activities in this category: aggressive grooming, social grooming, crawl across, were too low to permit reliable statistical analysis. However, aggressive grooming was found rather frequently in 1 and 2 month old isolated animals which had been tested against group-reared animals. In other animals, isolated and group-reared, it was almost completely absent.

Summary. Isolated animals performed less social contact behaviours, especially at early ages, when confronted with isolated partners than when confronted with group-reared rats. Only holding on was performed fairly frequently by them during the first three test ages. With increasing age the frequency of occurrence of social contact activities decreased, and differences between the distinct groups also waned.

Sexual behaviour

Frequencies of mounting and elevated crouching were too low to permit statistical analysis. In all encounters in which isolated animals were involved, mounting was very infrequent.

Only group-reared animals mounted their group-reared partners. This occurred occasionally during the playful interactions at an age of 1 month.

Antagonistic offensive activities

Push over and backward. Isolated animals pushed over their partners more often than group-reared ones did. Although no effect of the test partner was found, the significant rearing x partner interaction indicated that the isolated animals pushed over their group-reared partner more often. Pushing over and backward occurred very often during the first two test ages, thereafter it was observed very infrequently. In G-Gu encounters it was almost totally absent.

Keep down. Isolated animals kept down their partners more often and they spent more time on it than group-reared rats did. In the confrontations between isolated and group-reared animals, the isolated animals tended to keep down the group-reared animals more often than vice versa. Keeping a partner down was a favourite activity during the initial test ages,but decreased gradually to a low level of occurrence by the final three test ages. In G-Gu confrontations it rarely occurred, except at the age of two months.

Strike. No effect of rearing condition on the behaviour element strike was found. A group-reared rat was struck more often than an isolated animal. The significant rearing x partner interaction revealed that isolated animals especially struck the group-reared rats very frequently. In isolated-isolated pairs the element occurred rarely. During the initial two test ages striking was rather

frequent, but by later test ages it occurred only infrequently.

The other elements in this category: fight, bite and threat, were not observed often enough to permit statistical analysis. Fighting however, did occur in all I-I encounters, except in one pair at the age of 4 months. In I-G encounters about 50% of the animals fought, whereas only 4 pairs of G-Gu animals fought. Isolated animals also were the only ones which bit their partners. Threatening and sideways attack were observed very rarely and almost exclusively in isolated animals when confronted with a group-reared rat. Pull, a mildly aggressive activity, having a low level of frequency, was performed almost exclusively by group-reared rats.

Summary. During the first three test ages isolated animals exhibited a high level of dominance behaviour in comparison with group-reared rats. Strong offensive aggressive activities were almost exclusively present in isolated animals. Group-reared animals were rarely seen to perform offensive aggressive activities. Only striking and pulling, mild and rather playful aggressive activities, were observed fairly often in 1 and 2 month old group-reared rats.

Antagonistic defensive behaviour

Evade. Isolated animals evaded more often than group-reared rats did. A group-reared rat was evaded more often than an isolated animal. Analysis of the significant rearing x partner interaction revealed that isolated animals, confronted with a group-reared partner, had a high level of evading. Evading behaviour declined gradually in all groups with increasing age.

Retreat. The analysis of variance showed an interaction effect of rearing x partner. Isolated animals retreated from group-reared partners more often than from isolated ones. Group-reared animals retreated more often from isolated partners than from group-reared ones. The age-effect found, indicated a decrease in retreating behaviour with increasing age. During the last four test ages, retreating in all groups was observed very infrequently. The I-G animals showed a very sharp decrease during the first two test ages, whereas the decline in the other groups was much more gentle.

Keep off. Lying group-reared rats kept off their partners more often than isolated rats did. An isolated partner was kept off more often than a group-reared one. Group-reared rats kept off their isolated partners very often, notably at the age of 1 month. Thereafter the frequency of occurrence of this activity decreased to a low level. Although the difference at the age of 1 month found for different test partners was very large, as early as the second test month the difference had disappeared completely.

Fall sideways or backward. The activity fall sideways or backward occurred fairly often during the first two test ages, thereafter it decreased to a low level of performance. As became obvious from the analysis of variance, isolated partners induced falling sideways or backward in group-reared animals more often. G-Gu animals fell down only rarely. At the age of 1 month isolated animals caused the group-reared rats to fall sideways or backward rather frequently.

Sideways defensive posture. Isolated animals performed this activity more often than group-reared rats did. Differences in the time spent were even greater. A gradual decrease in occurrence was observed as the animals grew older. The significant rearing x partner interaction indicated the high incidence of the sideways defensive posture in the I-G encounters.

The other activities: kick, sitting defensive posture, full submissive posture, withdraw have not been observed often enough to permit reliable statistical analysis. The full submissive posture, however, was performed fairly often by I-I animals during the first three test ages. In encounters between isolated and group-reared rats, the group-reared animals exhibited the posture during the first three test ages fairly often too. In isolated animals in the I-G encounters it was almost absent, as it was in G-Gu encounters as well. It also should be mentioned that the activity freezing -i.e. cataleptic freezing posture- has been observed in both I-I and in G-I animals at various ages for a considerable amount of time. It has never been observed in isolated or group-reared animals confronted with a group-reared partner.

Summary. Isolated animals often evaded and retreated from group-reared partners, thus avoiding contact. Group-reared animals kept off their partner more often and fell down more often. In encounters between isolated and group-reared animals defensive activities were especially frequent. Most often they were seen in the group-reared animals. In the confrontations between two group-reared animals a very low level of defensive activity was observed.

Antagonistic ambivalent behaviour

Upright contact posture. Neither rearing condition nor test partner had any significant effect on the frequency or time spent on this activity. However, an interaction effect did exist between rearing condition of the test animal and that of the partner. Group-reared animals and isolated rats in the I-G interactions performed this posture fairly often, whereas in I-I and G-Gu confrontations it occurred very infrequently. As the animals grew older, the frequency of occurrence of the posture decreased to a very low level.

Parry. Isolated animals elicited more parrying behaviour in their partners than group-reared ones did. Group-reared rats, when confronted with an isolated animal, often parried. A gradual increase in frequency and time spent was observed up to an age of 3 or 4 months. Thereafter a decline was observed. During the first three test ages I-I animals spent a fair amount of time on parrying. At later test ages I-G animals parried more often.

Observation scores on boxing and standing attention were not high enough to permit statistical analysis. Therefore no statements concerning these activities could be made.

Summary. During early ages the ambivalent upright contact posture occurred almost exclusively in the isolated-grouped encounters. Because the behaviour in the I-G interactions is almost always symmetrical, isolated and group-reared animals spent an almost equal amount of time on the activity. Group-reared partners also spent a lot of time on parrying when confronted with an isolated partner. In G-Gu encounters both activities were almost completely absent.

Non-social behaviour

Exploration. Isolated animals initiated explorative behaviour less often than group-reared rats, they also spent less time on exploration. Exploration time tended to increase with increasing age. The analysis of variance revealed an interaction effect of rearing x partner. Group-reared animals, confronted with a group-reared partner, initiated exploration bouts most often and spent by far the most time on it.

Locomotion. Any means of locomotory progression, except dally, has been lumped under the heading locomotion. Isolated animals performed locomotory activities less often than group-reared animals. The G-Gu confrontations led to the most frequent locomotion. A slight decrease was found in all groups as animals grew older. The isolated animals, confronted with an isolated partner, exhibited the least amount of locomotory behaviour.

Sit. The analysis of variance revealed that isolated animals initiated sitting behaviour more often and spent more time on it than group-reared rats. Sitting was very frequently seen in confrontations between two isolated animals. The time spent on sitting tended to increase with age in confrontations in which isolated animals were involved, whereas the frequency showed a slight decrease. In the G-Gu interaction the time spent on sitting was rather low and remained almost equal at all ages. The time spent on sitting was most prominent in I-I interactions.

Groom. No effect of rearing condition on the frequency of grooming or the time spent on it could be found, although the effect on time spent approached significance. However, grooming lasted longer in animals confronted with an isolated partner than in those exposed to a group-reared animal. Group-reared rats confronted with an isolated animal spent most time on grooming. Frequency of grooming and time spent on it show a slight increase with increasing age.

Stretched attention. This activity was often seen in animals which hesitated to leave the relatively sheltered small compartments for the observation area. A difference in frequency of occurrence was found in relation with the presence of different test partners. In the confrontations in which an isolated animal was the partner, the element was observed most frequently, especially in group-reared animals. There was an increase in the frequency of occurrence of the posture with increasing age. At early ages it did not occur frequently.

Other non-social activities have not been observed very frequently, and therefore no reliable statistical analysis could be performed. It should be mentioned that beyond the age of 2 months, isolated animals spent a considerable amount of time in licking wounds. Wounds always consisted of bleeding broken nails as a result of the vigorous fights in which isolated animals became involved.

Summary. In general, group-reared animals were superior on non-social behaviour elements, such as exploration, locomotion and grooming. However, isolated animals spent far more time in sitting.

II.4.2. Discussion

An analysis and interpretation of the results gathered, together with additional qualitative observations, lend support to the hypotheses formulated by Welch and Welch (1969), Cairns and Nakelski (1970, 1971) and Banerjee (1971) in their studies on isolation in mice. These authors have stated that isolation-induced aggression is possibly of a reactive, "irritable" kind: animals isolated for some period during development tend to be hyperreactive and exhibit hypersensitivity to rather mild normal environmental stimulation, e.g. a conspecific partner. In the present study the differences in aggressive behaviour between isolated and group-reared animals were extensive. On the offensive side remarkable differences were found with respect to strong aggressive elements. Considerable differences existed with respect to the element immediately preceeding actual fighting, such as threat, attack and bite. These elements, almost totally absent in group-reared animals, appeared fairly often in isolated animals. Moreover, isolated animals fought more often than group-reared rats. The results indicate that in the confrontations between isolated and group-reared animals fighting was invariably initiated by the isolated animals. Isolated animals displayed push over and keeping down toward their partners more often too. The isolated rats seemed very reluctant toward approaches leading to contact, such as investigation, anogenital inspection, social grooming and attempts at mounting the partner. They invariably reacted hyper-aggressively. At younger ages at least the rearing condition of the test partner appeared to be important. Confrontations in which two isolated animals were in-

volved, inevitably led to vigorous fighting. Isolated animals confronted with a group-reared partner fought less often, although they spen. far more time in social contact with the group-reared partners (p 117).
This difference may be an indication of the appeasing role of the group-reared partner. Obviously, the behaviour of the group-reared animal prevents the interactions between an isolated and a group-reared animal from escalating into serious conflicts At the age of 1 month, no more than 1 out of the 10 I-G pairs actually fought. At later ages fighting occurred in about 50% of the I-G confrontations. At the age of 5 months, however, every I-G confrontation resulted in vigorous fighting. At first sight this finding seems to be contradictory to the assumption already made in respect of the appeasing role of the group-reared rat, in confrontations between an isolated and a group-reared animal. However, it is possible that short-term isolation does not bring about such disastrous effects as long-term isolation. A prolonged period of isolation may perhaps have such deleterious effects on the isolated animals as to eliminate the appeasing role of the group-reared partner. Evidence in favour of such an explanation is presented below (p 101 and 114). Therefore it is possible that, despite the appeasing role of the group-reared partners, about half of the interactions between isolated and group-reared rats at later ages result in vigorous fighting. It cannot be excluded that other factors may also be partly responsible for this result, e.g. endocrinological changes as a result of sexual maturation. With respect to activities in the category antagonistic defensive behaviour, analysis has revealed that group-reared rats tested against an isolated partner, performed most of the elements of this category far more often than group-reared rats confronted with a group-reared partner, or isolated animals confronted with either an isolated or a group-reared partner. Defensive reactions were seldom performed by isolated animals or by group-reared rats confronted with a group-reared partner. At younger ages the differences were greatest. Isolated rats reacted to an approaching testpartner either with freezing or strong aggressive behaviour. The same extreme reactions were noticed in isolated animals following the initial exploration sessions, when the rats had to be transferred from the observation cages back to their home cages. The isolated animals were extremely difficult to catch, running franticly through the cage, leaping with loud squeals, no doubt trying to escape. At last they sat "frozen" in a corner, often with teeth-chattering or emitting long ultrasonic noises. They invariably

attacked the hand of the experiment r and vigorously tried to bite. Remarkably, a fight involving isolated animals did not subsequently result in complete avoidance behaviour. Even after a severe defeat the animals tended to approach each other over and over again, and this often resulted in renewed fighting. The approaches became very slow however, usually with the bodies fully stretched. An attending response of the partner frequently led to evading or freezing behaviour in the approaching isolated animal. The partner thus seemed to be both simultaneously an extreme fear-inducing stimulus, as well as being extremely attractive. The behaviour displayed may be a reflection of a motivational conflict between a tendency to approach and a tendency to withdraw. Such a conflict may result in successive ambivalent behaviour (Schneirla, 1966).

The impaired initiative toward social contact behaviour in isolated animals, was reflected by the observations made in the social-attentive-at-distance category. The elements in this category are often introductory to social contact. Isolated animals did not initiate contact as often as group-reared rats did, the group-reared animals being superior on approaching their partners. Furthermore, an isolated partner was not approached as often as a group-reared one. The interactions between two isolated animals were rather infrequent. Confrontations between an isolated and a group-reared rat led to the highest degree of social contact. Isolated animals were superior in attending and evading behaviour. These elements again reflect the conflict between the tendencies to approach and to withdraw. The elements were most often performed in an alternating sequence, and most of the time the animals kept at some distance from each other. A remarkable qualitative difference existed in approaching behaviour between I(I)' and I(G) rats. The often slow, hesitant approaches observed in the I-I pairs were almost absent in the I(G) animals. The I(G) animals seemed rather uninhibited and equalled the group-reared rats in frequency of approaches. The tempo at which behaviour activities were performed also seems to be of importance. The I(G) animals were very hyperactive indeed, and their ongoing activities constantly changed every few seconds. The relative frequent occurrence of the element dally at the age of 1 month in contrast with group-reared rats, may also be interpreted as an indication of the hyperactivity. The G(I) animals were also caught by the whirling tempo of performance of the isolated animals during the early test ages. The figure representing the mean number of changes in behaviour, provides evidence for this deduction (p119). How-

ever, by the ages of 5 and 6 months G(Gu) animals became superior on this measure. Group-reared animals confronted with isolated partners behaved very cautiously at later test ages, presumably because of the rapid appearance of fighting behaviour in isolated animals by this time. A group-reared test partner tended to elicit investigating behaviour more often than an isolated animal, but the isolated animals spent more time on investigating behaviour. Since no difference in frequency was discovered, this implies that isolated animals investigated their partners for a longer period of time whenever they performed the activity. The isolated animals did not perform anogenital inspection very often and a sharp decrease was found with increasing age. In the group-reared rats however, a considerable increase was found as animals grew older. This finding is in accordance with results reported by Allen and Boice (1971) and Spevak et al. (1973). This behaviour pattern is probably a rather intimate one, coming as it does at the end of the investigation sequence, and is inhibited in isolated animals because of fear- induced interruption of the sequence. The studies of Hard and Larsson (1968), Spevak (1973) and Duffy and Hendricks (1973) concerning the effects of isolated rearing on male sexual behaviour, proved that elements belonging to the end of the male sex sequence -intromission and ejaculation- were impaired as a result of isolated rearing. However, no effect was observed in respect of the introductory elements such as climbing or clasping.

In respect of the elements in the social contact category, the relative high frequency of performance of aggressive grooming during the first two test ages in I(G) animals would seem to be important. This finding, together with qualitative observations may lead one to surmise that an escalation into fighting became inhibited by the reactions of the group-reared animals, which had probably often experienced this kind of intimate physical stimulation during "play" activities with their cage-mates. In the I(I) pairs aggressive grooming was observed only incidentally and invariably led to fighting because of the extremely intolerant reactions of the isolated partners.

Turning to the differences in non-social activities, the difference found in sitting behaviour would also seem to be of importance. Isolated animals spent more time on sitting. The element sit reduces to the freezing behaviour in a sitting position

and is synonymous with the crouching posture of Grant and Mackintosh (1963). Since there were no differences in the times spent sitting in the small compartments immediately after opening the sliding doors, -an indication of an equal effect of habituation in all groups- the difference found reflects the freezing behaviour in the dyadic test. Thus isolated animals froze significantly more. The observations of this parameter lend support to the findings of increased emotionality reported in other isolation studies (Dolger, 1955; Koch and Arnold, 1972; Cairns and Nakelski, 1970; Luciano and Lore, 1975).

In summary one may conclude that the rearing conditions of test animal and partner are important influences upon the behaviour of the animals. Isolated animals find themselves in a state of extreme ambivalence: they are almost irresistably attracted to the conspecific partner but at the same time are very disturbed and fearful. A similarly placed isolated test partner seems to strengthen the feelings of uneasiness, resulting in extreme "cut off" postures (Chance, 1962) such as the full submissive posture, cataleptic freezing and crouching. A rapid escalation into fighting and biting, the most extreme offensive acts, occurs where contact is unavoidable. Finally the original unstable equilibrium between the tendency to approach and the tendency to withdraw moves into the withdraw direction, although the isolated animals continue to approach each other, however hesitantly. On the other hand a group-reared partner, by his behaviour, tends to prevent the feelings of uneasiness from snowballing, and hence mild "cut off" postures such as withdraw, evade and sideways defensive posture, predominate over fighting.

The balance between approach/withdrawal tendencies in isolated rats confronted with a group-reared partner, does not move in either direction, resulting in continuous rapid alternations of approaching and retreating activities. This interpretation seems to be valid with respect to the first three test ages only. The increasing percentage of the I-G interactions which result in fighting as age increases, probably reflects the enhancement of debilitating consequences as a result of prolonged periods of isolation. Therefore it would not be unreasonable to assume that at later ages, i.e. beyond the age of 3 months, the deleterious effects have become so disastrous and so compelling as to more or less rule out the influence of the group-reared animals, thus making the development and result of the interactions less dependent on the behaviour of the partner. This assumption is supported by

studying the latencies of early fighting. At the ages of 1, 2 and 3 months fighting was observed sooner in I-I pairs than in I-G pairs (mean latency scores: 436 sec.- 789 sec. (1 month); 223 sec. - 420 sec. (2 months); 193 sec. - 310 sec. (3 months)). At later ages the differences disappeared (mean latency scores: 293 sec. - 268 sec. (4 months); 263 sec. - 285,5 sec. (5 months); 452 sec. - 301 sec. (6 months)). Moreover, it seems plausible to assume that prolonged periods of isolation push the balance over into the withdrawal direction, thus resulting in avoidance behaviour. This last assumption is validated by the sharp decrease in time spent in social behaviour with increasing age, and by the fall in the index of behaviour change (p 118)discovered in the confrontations between isolated and group-reared animals.

Confrontations in which two group-reared animals were involved and where the pair was unfamiliar with each other, almost always proceeded harmoniously. From the first test age onwards these rats spent most of the time in non-social activities. Qualitative observations of the behaviour of unfamiliar group-reared pairs do not justify an interpretation of the lack of social contact in terms of active avoidance existing between the animals. The animals simply seem to be more interested in the environment than in the partner. Although they approach each other rather often, they do not spend much time on social contact.

Several authors (Gruendel and Arnold 1969, 1974; Gerall et al. 1967; Spevak, 1973) have stressed the importance of social experience in the early postweaning period for the development of normal social (sexual) behaviour. "Play" activities with peers during the juvenile and preadolescent periods are especially thought to be important for the development of appropriate responses and reactions to the behaviour of littermates. The results in the present study, in which the animals were isolated immediately after weaning, seem to support these assumptions. The finding that even at a very young age an isolation period of only one week had large debilitating consequences was very striking indeed. The period mentioned may indeed be a very sensitive one for the development of social behaviour.

The means by which socialization is effective in reducing, or social isolation is effective in producing aggressive behaviour still remains the object of dispute. The explanation given by Ward and Gerall (1969) in terms of response hierarchies,

containing the statement that group-reared animals have larger response repertoires because of social experience, is in contrast with the results of the present study. On the contrary, the behaviour repertoire of the isolated animals contained more elements, and experience seemed to be of minor importance. The development of an aggression inhibiting olfactory substance acting as a primer pheromone, and the gradual decrease of emission of the pheromone in isolated animals, has been postulated by Harmatz et al. (1975). Their hypothesis is not easily reconciled with the findings presented in the first, qualitative study, where group-reared animals fought heavily when they had reached adulthood. Moreover, it seems doubtful that only 25 day old group-reared rats are capable of emitting aggression inhibiting pheromones, the function of which is immediately clear.

Scott (1966) hypothesized that the difference in aggressive behaviour between group-reared and isolated animals might be best explained by a process of "passive inhibition" resulting from grouped-rearing: animals build up a habit of non-fighting simply by not fighting and this habit becomes associated with certain environmental situations. The hypothesis does not have general validity. The severe and lethal fights among the group-reared animals during adulthood reported in the first study (p 64 and 65) are in obvious contrast with the assumption of Scott. If a process of "passive inhibition" is at work in developing group-reared animals, then other factors (e.g. endocrinological changes with increasing age or appropriate environmental stimulation) are able to counteract such a process.

Cairns and Nakelski (1971) in their excellent mice study, also concentrated on the changes in behaviour produced by grouped or isolated animals. They interpreted Scott's passive inhibition hypothesis in terms of either response competition or conditioned inhibition. The explanation in terms of response competition suggests that by grouped rearing an animal learns non-fighting social responses (e.g. social grooming, social investigatory activities) which become dominant over fighting responses. Aggressive activities (e.g. attack, fight) are then inhibited by competing social responses. The interpretation in terms of conditioned inhibition proposes that by grouped-rearing rats learn what behaviours they should avoid during interactions in order to prevent any possible harmful consequences associated with the performance of the behaviour before. Cairns and Nakelski found that

neither of these two explanations were satisfactory for interpreting the behaviour observed in isolated mice. The isolated mice appeared to be highly reactive to stimulation provided by a conspecific partner, but they also oriented toward, and investigated the partner more often. Cairns and Nakelski believe that group-reared mice become adapted to various forms of physical stimulation during development, and continue their ongoing activities such as eating, self grooming etc. despite disruption by a partner. Isolated animals however, become easily disrupted by interanimal stimulation and react sharply to the stimulation. The outcome of the interactions is dependent on the reactions of both partners.
The qualitative and quantitative data of our study provide evidence in favour of the assumptions of Cairns and Nakelski. In the test sessions of our study the group-reared animals showed more interest in exploring the environment than in investigating or grooming the partner. Qualitative observation of the behaviour of the group-reared pairs failed to convince us of the existence of a process of social-response competition able to inhibit aggressive behaviour.
Furthermore in our study no evidence could be found which would lead us to conclude that the animals in the small compartments fought fiercely and had thus experienced harmful consequences as a result of fighting. However, it remains possible that fighting did in fact occur, but in this case it certainly did not lead to any observable consequences such as wounds, bloodshed or avoidance behaviour. We are inclined to doubt the assumption in terms of conditioned inhibition.
The group-reared animals in our study showed little interest in each other, and even very young animals of 1 month old spent much time in exploring the environment, although they were engaged in social contact occasionally. They displayed the familiar "playful" activities of young developing rats interacting with each other. With increasing age, the time spent on social contact gradually diminished but the animals did not seem to avoid each other. The overt behaviour observed in isolated rats was totally different. Quite obviously the confrontation of an isolated animal with a conspecific, isolated or group-reared one, puts the isolated animal in a state of ambivalence. They become simultaneously irresistably attracted to and very frightened by the "novel object".
In isolated animals a very poor balance seems to exist between the tendency to approach and the tendency to withdraw, which results in a rapid and successive

transition from approach to withdrawal behaviour (for instance repeated attend-evade sequences). Behaviour elements in which both tendencies were simultaneously present -e.g. frozen sitting, hesitant approach behaviour or stretched attention- were also often observed. The isolated animals were apparently not able to gain control over their activities. The overt behaviour of isolated animals of all ages equalled the behaviour of the young normally developing group-reared rats of the socialization and early juvenile period (chapter I), displaying the same unbalanced performance and seeming to lack the ability to inhibit their behaviour.

A striking difference was observed between the interactions of group-reared animals and those in which an isolated animal was involved. The interactions in which an isolated animal became involved very often resulted in severe and heavy fighting, even at an early age. The rearing condition and age of both partners in a pair appeared to be important. With only one exception, any two isolated rats in a pair always fought, irrespective of their ages. About 50% of the confrontations between an isolated and a group-reared animal resulted in fighting. Fighting occurred more often at later ages among isolated - group-reared interactions. The isolated animals appeared to be hyperreactive to social stimulation. The state of hyperexcitability and hypersensitivity, obviously tended to prevent the isolated animals from reacting appropriately to the behaviour of a partner. The extremely fearful reactions of the isolated animals to rather mild social stimulation e.g. being investigated or groomed- increased the probability of fighting.

Another characteristic of the behaviour of isolated animals was the fact that even after harmfull fighting and a severe defeat the isolated animals continued to approach the partner over and over again. The isolated rats seemed to lack the ability to inhibit the tendency to approach, and to learn from experience by showing avoidance behaviour.

In our opinion, the aggressive behaviour observed in isolated rats seems to be the result of the inability of the animals to adapt to the behaviour of a partner, and to respond normally. The aggression is thus of a reactive, irritative kind. It is very tempting to correlate the results found in respect of the behaviour of isolated rats, with findings on neurophysiological and neurobiochemical functioning as a result of isolation. Evidence has been presented that the adrenergic

system, known to be involved in behavioural arousal, is indeed affected by the process of isolation. Welch and Welch (1969) revealed that the slower rate of noradrenaline turnover and release on the noradrenaline receptors, found in isolated mice, leads to a hypersensitivity of the receptors, resulting in lower thresholds in isolated animals for central sympathetic excitability when stimulated by new environmental stimuli.

Avis (1974) found evidence of a noradrenaline mediated inhibitory system at work in isolation-induced aggression. Decreasing the norepinephrine transmission is assumed to increase aggression, while increasing norepinephrine transmission inhibits aggression. The turnover of norephrine is less in isolated aggressive mice and may lead to a nonspecific "untuned" response, which is possibly what has been termed irritable aggression (Avis). Essman (1971) showed that functional denervation of non-specific somatosensory pathways as a result of social isolation leads to cellular threshold changes in mice. Melzack (1969) working with dogs, presented evidence of excessive arousal of the central nervous system, probably because of a loss of the capacity to filter out irrelevant information at successive synaptical levels of sensory pathways, resulting from isolation. These findings may lend support to the explanation presented at the behavioural level in the present study. Whether the cholinergic inhibitory system plays a role in respect of the lack of inhibitory ability observed in isolated rats is also an important question. Valzelli (1973) has also found evidence of impaired cholinergic transmission as a result of isolation.

It would be very interesting to investigate a possible correlation between the development of the cholinergic inhibitory system, known to mature during the 4th postnatal week in rats (Fibiger et al., 1970; Campbell and Mabry, 1972) and the sensitive period for social isolation in rats. Possibly the process of isolation has consequences for the functional properties of the developing inhibitory centres.

II.4.3. Unfamiliarity; Isolation; Age

The second analysis of variance has been performed in order to investigate:

a) the influence of familiarity or unfamiliarity of a group-reared partner on the behaviour of a group-reared rat;

b) the relative importance of unfamiliarity or isolation per se, being the two intrinsic components of an isolated partner with which a group-reared rat is confronted. In isolation studies the two variables are usually confounded

An isolated rat, a group-reared rat meets firstly, is not only an animal which has been isolated but also one that is unfamiliar. In an effort to unravel these two factors, the effects of isolation and of unfamiliarity will be compared. The behaviour of the group-reared rat confronted with either an isolated or an unfamiliar group-reared rat, is the point of reference.

The effects of different rearing conditions -isolated versus grouped-rearing- have been investigated and discussed in the first analysis of variance. They will therefore not be referred to in the discussion of the second analysis of variance.

Familiarity versus unfamiliarity; Age

The time spent on behaviour elements together with the means of their frequency of occurrence are tabulated in tables 8 through 11 of the appendix. Figures of various elements and tables of the results of the analysis of variance are printed in the appendix on pages 152 through 166.

Social exploration

a) attentive-at-distance

Approach. Any influence of familiarity or unfamiliarity on the number of approaches of group-reared rats has not been found. The number of approaches decreased gradually and equally with increasing age in both G-Gf and G-Gu rats.

Follow. The two groups did not differ in following the partner. With increasing age following behaviour decreased gradually to a rather low level of performance.

Attend. Group-reared rats did not attend differentially to a familiar or an unfamiliar group-reared partner. Attending was also performed virtually equally often by both groups at all ages.

Summary. No influence of familiarity or unfamiliarity of the partner has been found on the social-attentive-at-distance behaviour of group-reared rats. Attending at later ages did result in increasingly less approaching or following behaviour.

b) in physical contact

Investigate. The analysis of variance revealed that familiarity or unfamiliarity of the test partner did not effect the investigatory behaviour of group-reared rats differentially. There was a slight increase in investigatory behaviour with increasing age.

Oral inspection. Group-reared rats performed far more oral inspection behaviour if tested against unfamiliar rats than if tested against familiar partners. While oral inspection was performed at a low level in G-Gf animals at all ages, it increased with increasing age in G-Gu animals. Since this behaviour has not been displayed very frequently, the results should be interpreted with caution.

Nosing. The element nosing has not been observed very frequently. Unfamiliar rat pairs performed this behaviour more often than familiar ones. Since the element has been observed very infrequently, the result should be interpreted with caution.

Anogenital inspection. A highly significant effect of familiarity or unfamiliarity was found for the element anogenital investigation. Group-reared rats investigated an unfamiliar partner more often at the anogenital region than a familiar one. There was a sharp increase in the amount of time spent on anogenital inspection with increasing age, the increase in G-Gu animals being steeper than that in G-Gf rats.

The element crawl under has not been reliably observed often enough to permit analysis and interpretation.

Summary. In unfamiliar rat pair confrontations, more social investigatory behaviour was performed than in familiar rat pair confrontations. The difference in anogenital inspection was large. Differences existed with respect to nosing and oral inspection. These elements, however, were observed rather infrequently. Although the effect on investigating the partner did not reach significance, the difference between the groups was in the same direction.

An increase with increasing age has been found for all elements in the category social contact behaviour.

Social contact behaviour

Touch. The analysis of variance revealed that there was no effect of familiarity or unfamiliarity on touching the partner. Touching showed a decrease after an initial fairly high level of performance. At later test ages a slight increase did show up.

Take hold. No effect, whatsoever, has been found on the element take hold. Beyond the age of 3 months the element was not observed very frequently.

Hold fast. The element has been observed in both groups very infrequently at all ages. The element was therefore precluded from analysis.

Summary. No influence of familiarity or unfamiliarity has been found on behaviour elements falling in the social contact category.

Sexual behaviour

No difference whatsoever existed with respect to mounting behaviour. The element has not been displayed very often, and even decreased with increasing age.

Antagonistic offensive behaviour

Strike. There was an effect of familiarity on the time spent on striking behaviour, but not on its frequency. A group-reared rat confronted with a familiar group-reared partner spent more time on striking than if confronted with an unfamiliar rat. The element has been observed with decreasing frequency as age increased. By the last two test ages it had almost disappeared.

The other elements in the antagonistic offensive behaviour category have not been observed at all, or to such a low degree that no statistical analysis could be performed. In the present study, antagonistic behaviour between group-reared rats, familiar or unfamiliar, was rather exceptional.

Antagonistic defensive behaviour

Evade. No effect of familiarity or unfamiliarity of the testpartner on evading behaviour of group-reared rats has been found. A gradual decline with increasing age was found for this element.
Retreat. The two groups did not differ with respect to retreating behaviour. Except for the first two test ages, retreat has been observed infrequently.
Keep off lying. No effect of familiarity or unfamiliarity on keeping off the partner has been found. The significant familiarity x age interaction on the frequency measure, indicates the differential decrease in keeping off between the two groups with increasing age. The decline in G(Gf) animals was much steeper than in G(Gu) animals where the decline was of a gradual nature.
Sideways defensive posture. The groups did not differ with respect to the sideways defensive posture. A gradual decline in both groups has been found with increasing age.

The other elements in the defensive antagonistic behaviour category have been observed very infrequently or not at all.
Summary. No effect of familiarity or unfamiliarity of the testpartner on the defensive antagonistic behaviour of group-reared could be detected. In general, the time spent and the frequency of occurrence of elements in the category showed a gradual decline with increasing age.

Antagonistic ambivalent behaviour

The elements in this category have been observed so infrequently as to make reliable statistical analysis and interpretation impossible.

Non-social behaviour

Exploration. Both G-Gf and G-Gu animals spent a great deal of time on explorative behaviour at all ages. Neither familiarity nor unfamiliarity of the partner had any effect on exploration.
Locomotion. No effect of familiarity or unfamiliarity of the partner on locomotory behaviour of group-reared rats has been found. Locomotory activity tended to decrease with increasing age.

Groom. The two groups did not differ with respect to grooming behaviour either. The time spent on grooming behaviour increased with increasing age, although frequency of initiating a grooming bout remained about equal. It should therefore be concluded that at later ages the group-reared rats continued a grooming bout for a longer period of time.
Sit. No effect of familiarity or unfamiliarity of the testpartner on sitting behaviour could be detected. The time spent on the activity remained equal at all ages. The scores for sitting behaviour reduces to the "frozen" sitting in the small side compartments immediately after opening the sliding doors to the big compartment of the observation cage.

Other non-social activities seemed of minor importance in discussing different reactions of group-reared rats to familiar or unfamiliar partners and were therefore precluded from analysis.
Summary. No effect of familiarity or unfamiliarity of the testpartner on the non-social activities of group-reared rats has been found. Age did exert differential influences on the various elements in the category.

II.4.4. Discussion

The only persistent differences between G(Gf) and G(Gu) animals are related to the behavioural activities in the category headed "social exploration behaviour in physical contact". Unfamiliar animals initiated social exploration activities in physical contact more often and spent more time on them.
A highly significant difference existed with respect to the behavioural element anogenital inspection, especially at later ages. The familiar animals showed no increase in mean total time spent on this behaviour, beyond the age of 3 months. while unfamiliar ones spent increasingly more time on this activity with increasing age, resulting in considerable differences between the groups at the test ages of 4, 5 and 6 months. According to a number of investigators rats are capable of recognizing a stranger (Steiniger, (1950); Barnett, (1963, 1964); Husted and McKenna (1966); King and Dua (1971); Galeff (1970); Alberts and Galeff (1971, 1973)). All authors hypothesize that olfactory cues play a role in this process of recognition. Since it is known that rats emit pheromones, which may have a function as social communicative substances (Gleason and Reynierse, (1969)), the

difference found in the present study supports this hypothesis. Pheromones are emitted in the urine as well as by glands in the anogenital areas. The differences found may indicate that anogenital inspection is an important activity in the process of recognition because of the information it provides about the partner. Moreover, it is interesting to note that beyond the age of 2 months, familiar animals do not any longer show an increase in the time spent on this activity and that considerable differences between the familiar and unfamiliar groups existed beyond the age of 3 months. This may indicate that the process of recognition and thus emission of the pheromones, crucial to this process, starts somewhere between the ages of 2 and 3 months. Male rats reach sexual maturity somewhere between these ages. In future investigations it will be of importance to explore the possible relationship between the emission of pheromones correlated with attaining sexual maturity and the process of recognition. For the time being it is interesting to note that Mugford and Nowell (1970, 1971) in studies with mice found that androgenic substances (e.g. testosterone propionate, a male sex hormone) are in fact emitted in the urine and by the preputial glands and act as aggression-evoking substances. This finding leads to the question of why in the present study, group-reared animals, familiar and unfamiliar, did not fight at all or only incidentally. Firstly, consider the familiar rat pairs. In contrast to the animals of the first study living in the seminatural environment, which fought vigorously after reaching adulthood, the animals in the present study did not fight. Obviously an important difference of developmental environment exists between the two investigations. The animals used in the present experiment were raised in a rather small laboratory cage in groups of 4 males. The cage is probably too small to permit the build up of an individual territory which has to be defended against the other cage mates, or from which other rats could be expelled. Moreover, in our study females were absent throughout development. Barnett (1964) assumes that the presence or absence of females among groups of male rats may be an important factor for the elicitation of territorial aggression between males. In our study even the groups which lived together for 6 months provided no indication whatsoever with respect to the building up of a territory by one of the animals nor with respect to a dominance hierarchy appearing within the group.

The following remarks may be made concerning the testing procedure. First of all, it seems valid to draw the conclusion that the time allowed for exploration of the test environment (3 x 2 hrs.) is, perhaps, too short to build up a territorial "sense" in the animals. The time spent in exploration during the test session is rather high. The possibility of the test cage being too small to permit the maintainance of a territory seems invalid, since investigations on the so called "home cage" effect have demonstrated that rats do defend their own, even very small, living cages against intruders. The possibility that the observation time of 15 minutes is rather short for induction of aggression, cannot be excluded either.

With respect to the unfamiliar rat pairs, it is obvious that the animals recognize the partner as a stranger. However, in contrast to the findings of Barnett (1963, 1964), Galeff (1970), Calhoun (1962) and Steiniger (1950), among others, in the present study the recognition did not end in fighting bouts between two unfamiliar animals. Probably the absence of the first of the two conditions mentioned by Barnett (1964) as being of great importance for territorial "home-cage" aggression (i.e. familiar environment and unfamiliar intruder) inhibits aggressive behaviour during the test sessions. Some behavioural indications of a slight increase of mildly aggressive activities were found in the unfamiliar pairs, especially at later ages. Activities in the category headed "ambivalent behaviour" also increased slightly with age in the unfamiliar pairs, whereas they were almost totally absent in the familiar pairs. The remarks made with respect to the familiar pairs hold true, of course, for the unfamiliar ones too.

The results with respect to the other activities in the category "social exploration in physical contact behaviour" underline the tendency of unfamiliar animals to spend more time upon these activities, as well as initiating them more frequently. Unfamiliar animals spent significantly more time on oral inspection and nosing. The time spent on oral inspection increases with increasing age in the unfamiliar animals. The differences found in these activities, especially nosing, should be interpreted with caution, since they have not been observed very frequently. However they point in the same direction as the differences found with anogenital inspection. Unfamiliar animals also tended to investigate each other more often than the familiar ones did, as is indicated by the considerable, yet non-significant

difference found. In the unfamiliar pairs the time spent on this activity increased steadily with age, whereas in the familiar ones no increase was found beyond the age of 2 months. Barnett (1963) also reports an increase in this behaviour which he calls recognition sniffing, in animals confronted with a stranger. In general, the results found are in accordance with those discovered in comparable earlier studies by the author (1972) using Tryon Maze Bright rats, and by Timmermans (1977), using rats of the Wistar Albino strain.

II.4.5. Isolation versus infamiliarity

In isolation studies, the factor isolation usually consists of isolation, per se, and of unfamiliarity. Normally these two factors exert their influence simultaneously. In an effort to unravel the relative importance of each of the factors, the results of the analysis of variance with respect to the values found for isolation or unfamiliarity have been examined further.
In general, it can be said that the factor isolation, per se, seems to be more important than the factor unfamiliarity. Isolation of the partner seems to be responsible for many of the changes in behaviour that exceed those induced by unfamiliarity. Very few significant F-values are found for unfamiliarity, whereas most of the F-values for isolation reached significance.Only in the case of significant F-values occurring for both isolation and unfamiliarity, has a further analysis been performed: in order to gain some insight into the relative importance of isolation and unfamiliarity, the true variances of familiarity (σ^2_β) and rearing (σ^2_α) have been estimated. This was done by reducing the mean square of the relevant source of variance by the error variance, and dividing by the coefficient of σ^2_α or σ^2_β as given in the model of expected mean squares (cf. p 86; 87). Rearing and familiarity had an effect on oral inspection and anogenital inspection (frequency and total time). With respect to oral inspection, the true variance of the factor unfamiliarity was 3 times that of isolation (1.49 versus 0.49). Therefore one may conclude that unfamiliarity seems to be more important for the element oral inspection than isolation. Since the true variances on anogenital inspection did not differ much, one might conclude that both factors are equally important (49.9 versus 43.5). Significant F-values were also found for nosing (frequency)

and strike (total time) for both isolation and unfamiliarity. The true variance on nosing was higher for isolation than for unfamiliarity (0.23 versus .06). Isolation seems to be more important. However, it should be noted that the observation of nosing was very infrequent. Since the true variances in time spent on striking for isolation and unfamiliarity did not show any difference (6.72 versus 6.97), it might be concluded that both factors are equally important.

II.4.6. Percentage of animals fighting

The most striking effect of isolation discovered in our investigations was the occurrence of hostile aggression in all I-I confrontations with the exception of one. Even a very short isolation period of 7 days resulted in adult-like frantic fighting with biting, leaping, attacking, teeth chattering, piloerection, cataleptic freezing and ultrasonic emissions. In the seminatural environment of the ontogenetic study (chapter I), serious fighting including the behaviour elements mentioned before, did not show up in the group-reared rats until they reached adulthood. Evidently, the short isolation period immediately after weaning, brought about a behavioural change in the young animals. At this age even a short isolation period is long enough to change body weight increase too (p 121) and has its consequences on brain weight parameters (v. Woerden, in press). One characteristic of the I-I confrontations was the fact that even after heavy fighting and a severe defeat, the animals were still attracted to each other and engaged in repeated fighting.

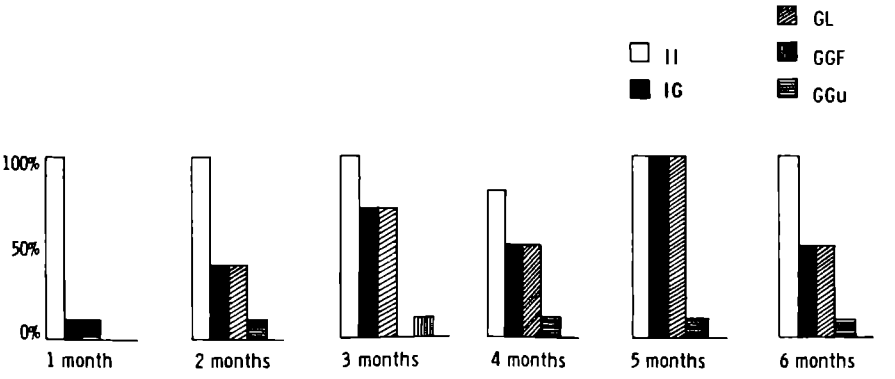


Fig. 25. Percentage of animals fighting per condition at different ages

Approaches, however, became hesitant and easily changed into evading or retreating behaviour before actual contact had been established. The I-G confrontations resulted in less fighting as measured by the percentage of fighting pairs. Fighting again was very vigorous. In these confrontations, it was almost always the isolated animal which started fighting as a result of a too intimate approach from the group-reared animal. Qualitatively, it seemed as if the isolated animals were put out of countenance by the partner's approach, and reacted with immoderate aggressive activities. They were rather intolerant toward group-reared animals, trying to make contact. On the other hand, the group-reared partners possessed a heavy power of attraction, leading to continually repeated approaches from the isolated animals.

In the G-Gf and G-Gu confrontations little fighting occurred. Of the familiar group-reared rats only one pair fought before the age of 3 months. The unfamiliar group-reared animals did not fight much more. This observation is in contradiction with the findings of Barnett (1963, 1964); Steiniger (1950); Calhoun (1948) and Galeff (1970), who reported that rats will always attack a stranger. However in our observation situation, the two animals are tested in a cage which is relatively unfamiliar for both of them. The three day exploration period may be too short to become fully acquainted with the test environment and to build up a territorial sense in the animals. The finding that familiar rat pairs did not fight at all at later ages is also in contradiction with our finding in the semi-natural environment (chapter I). The discrepancy between housing condition and observation box in the dyadic tests might be an explanation. It should be mentioned that during the whole period up to the age of 6 months, the animals housed in the macrolon cages in groups of 4, did not show any sign of territorial aggression. Furthermore, no wound scars could be detected. It seems that the housing condition prevents the development of events that can be observed in animals raised in semi-natural environments.

II.4.7. Reversibility of changes induced by isolation

A rather crude investigation was performed in order to study the lasting effects of isolation. The I-I pairs of the ages 1 month and 5 months were allowed to stay together in the observation cages for one week after the test session. The only parameters used to measure the long-term effects of regrouping the isolated animals, were the changes in body weight and the appearance of wounds. The animals were weighed daily. On the first day frequent non-systematic observations were also made.

The animals tested at the age of 1 month, showed a rapid decline in aggressive behaviour during the first day, although they spent a lot of time on social behaviour. The interactions between the young rats became more and more "playful" resembling that of group-reared animals of the same age. All the animals gradually gained body weight within the week, and after 5 days the mean weight gain was 18.33 grams, with a range of 16 to 23 grams. In all animals, weight gain started as early as day 1. No sign of wounding could be detected on any animal.

A different pattern of adaptation to regrouping was found in the older age group (5 months). These animals fought vigorously during the first day, resulting in severe wounds in 3 animals. All the animals received wounds to the nails of the toes. The wounds resulted in spontaneous avoidance between the animals for rather long periods. The stressful effect of regrouping at this age was indicated by the body weight measure. 6 Out of 10 animals lost weight on the very first day, ranging from 3 to 21 grams. One animal did not gain or loose weight, and only three gained some weight ranging from 2 to 6 grams. By the end of the week 5 animals were still under their original weight (range 2 to 21 grams), one animal had not changed and four animals had gained weight (range 3 to 9 grams). Three animals had signs of wounds, but no fresh wounds were found at the end of the week.

The results suggested that the deficits induced by isolation are only temporary at younger ages following a relatively short isolation period. The animals adjust to regrouping fairly rapidly at that age. However, at a later age, after a prolonged period of isolation, deficiencies seem to be much more lasting. Obviously, a prolonged period of isolation has greater consequences for social behaviour.

Cairns and Nakelski (1971) and Luciano and Lore (1975), report that the effects of isolation on aggressive behaviour are reversible. After regrouping mice (Cairns and Nakelski) or rats (Luciano and Lore), the animals show a sharp decline in aggressive behaviour. The same phenomenon was observed in our study with the older age group. However the decline seemed to be induced by mutual active avoidance by the members of the pair. The results should necessarily be interpreted with caution because of the rather crude meaures used. Detailed study might yield a more definite solution to the question of reversibility.

II.4.8. Social behaviour

All activities that implied interaction between two animals were lumped together to form the overall category social behaviour. The amount of total time spent on social behaviour declined with increasing age (fig. 26).

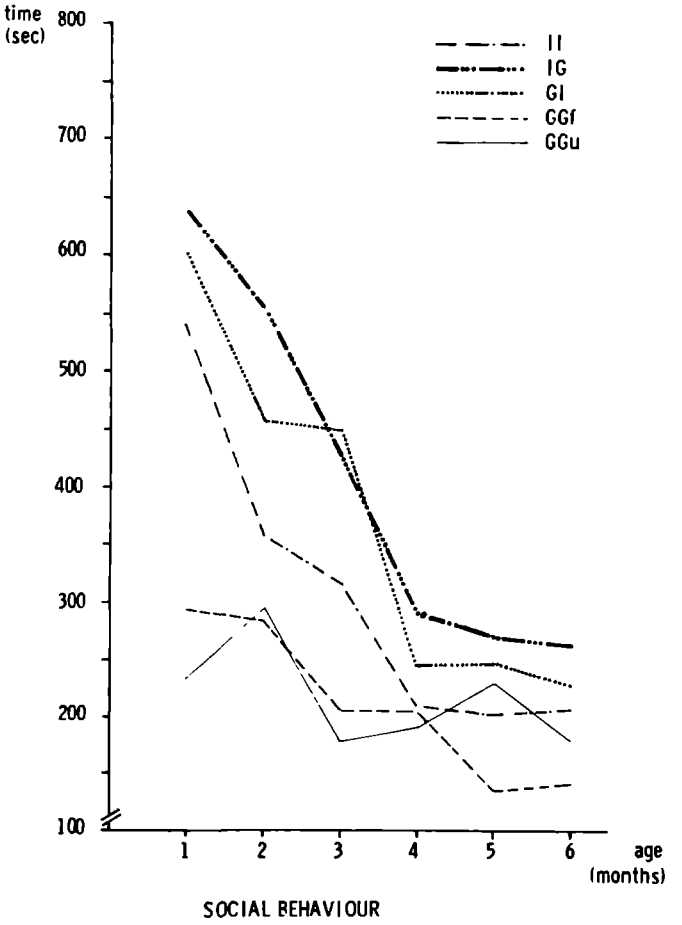


Fig. 26. Time spent on social behaviour by the various groups at different ages.

Initially, a fairly high proportion of the total observation time was spent on social activities. In particular, the I(I) the I(G) and the G(I) animals performed social behaviour for a relatively high percentage of time during the first three months. G(GF) animals do not differ much from G(GU) animals, although at later ages the unfamiliarity of the partners leads to an increase in social behaviour in the G(GU) group. G(GF) animals show a steady decline in social activities. It should be noticed that the amount of total time spent on social behaviour by the familiar group-reared rats in this test-situation differs from the amount of time the group-reared animals in the seminatural environment spent on social behaviour at the same ages (32.6%, 31.4% and 22.8% versus 24.8%, 16% and 15% at the ages of 1, 2 and 3 months respectively). This could be an indication of the fact that the test-situation used is a more compelling environment with respect to social behaviour than the seminatural environment.

II.4.9. Mean number of different behaviour patterns

The various groups tested, differ considerably with respect to the number of different behaviour patterns they perform at distinct ages. In all groups the number of changes in behaviour decreases with increasing age (fig. 27). The I(G) and G(I) groups change their behaviour very frequently at the ages of 1 and 2 months. Remember that these animals were tested against each other. The I(I) animals exhibit low frequencies for behavioural changes. Qualitatively, their overt behaviour at early ages, after a short isolation period, resembled that of unfamiliar adult group-reared animals. They were very cautious in making contact and they engaged in long investigation bouts. Moreover, they fought extremely vigorous for longer periods. They spent a lot of time in freezing or sitting behaviour after fighting bouts. The high incidence of changes in behaviour in the I-G animals therefore seems to be caused by the behaviour of the I(G) animals against which they were tested, The G(GF) and G(GU) animals show intermediate changes and do not differ very much. However, at later ages G(GU) animals display the highest number of changes in behaviour.

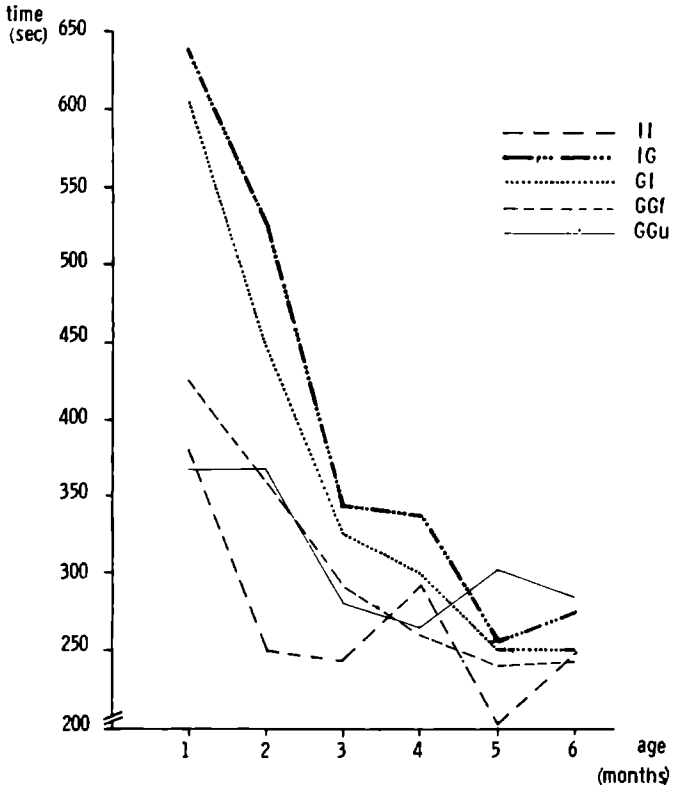


Fig. 27. Mean number of different behaviour patterns

The mean number of different behaviour patterns in this study differs very much from the scores in the seminatural setting. Evidently, this test situation seems to be more constraining for the animals as far as making contact with the partner and reacting to the behaviour of the partner is concerned.

II.4.10. Ultrasound emissions

Ultrasonic signals emitted by the animals have been recorded on audiotapes following transformation into audible signals, and have been synchronized with the behavioural parameters, recorded on videotape, According to Sales (1972a, 1972b) rats emit ultrasonic signals during aggressive encounters. The signals can be divided into two distinct types: a) short pulses at about 50 kHz and lasting from 3 to 65 msec. and b) long pulses at 20 to 30 kHz and lasting up to 3000 msec. In the present study ultrasonic signals were detected during all aggressive encounters which led to fierce fights between two rats even at the age of 30 days. Because of a lack of adequate equipment the transformed signals were distinguished by ear. This, however, could be performed easily, since after transformation a clear qualitative distinction still existed between the two kinds of signal.

Moreover, the transformation used did not produce a change in the duration of the pulses.

The short pulses at high frequencies were emitted in correlation with the behavioral activities approach, attend, hold on, sideways offensive posture, attack, touch, aggressive grooming and push over. These elements were performed immediately before or after fighting.

The long pulses at lower frequencies were emitted simultaneously with activities such as full submissive posture, keep off, freezing, sit, upright sit and upright defensive posture.

After a critical analysis of the data presented by Sales, Bell (1974) suggests that the distinct signals reflect the state of arousal in the animal emitting the ultrasounds. Short pulses would be an indication of a high arousal state, and long lasting pulses indicate a low state of arousal. Sales (1972a) believed that the different signals reflect a distinct motivation in the animal. Long ultrasonic pulses indicate a state of submission in the emitting animal, and short pulses reflect an aggressive motivation. The emission of the long pulses should lead to inhibition of aggression in the attacking animal. Bell, however, hypothesizes that emitting ultrasonic signals merely leads to establishing a similar state of arousal in the receiving animal.

In the present study no evidence could be gathered to sustain the assumption of Sales concerning the effect of long pulses, Although long pulses were emitted by both animals after fighting, they failed to prevent the outbreak of new vigorous fights between the animals. The explanation of Bell seems to be subject to objections too. There is no evidence whatsoever that freezing or sitting animals are in a state of low arousal. On the contrary, it may be assumed that the rats after being severely defeated are highly emotional and have a high arousal state. A more simple explanation may be valid. Since it is known that ultrasonic signalling correlates with respiration, notably expiration, the distinction might be an artefact of the state of overt behaviour. The kind of overt behvaiour sets its limits to the respiration rate, and this could be responsible for the two distinct ultrasounds. Short pulses correlate with some kind of activity that should be qualified as dynamic. Long pulses are correlated with behaviour patterns that should be qualified as relatively static.

II.4.11.Body weight

A differential development in weight gain between isolated and group-reared animals has been observed (fig. 28). At the age of 1 month, after no more than 7 days of isolation, a significant difference in body weight was found. The isolated animals weighed significantly more than the group-reared rats ($t = 4.9$, $p < .01$). At the age of 2 months the isolated animals weighed more too ($t = 6.1$, $p < .01$).

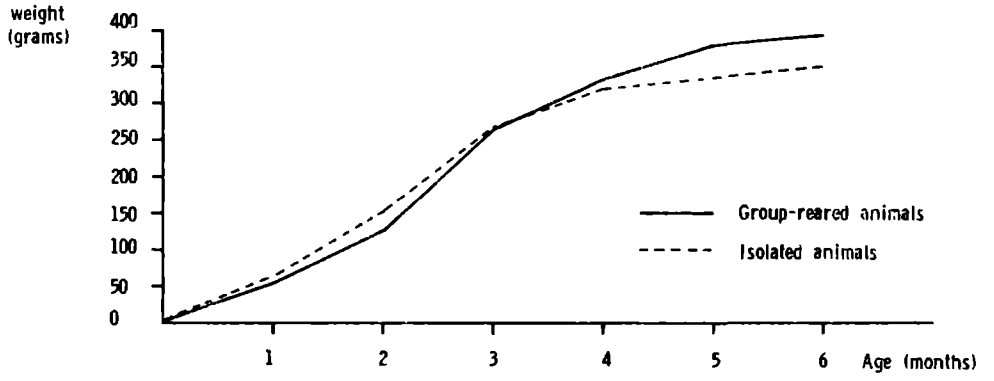


Fig. 28. Mean weights at different ages of the various groups

No significant differences in body weight existed at the ages of 3 and 4 months ($t = 0.3$ and $t = 1.3$ respectively). At the age of 5 months a significant difference again emerges ($t = 4.5$, $p < .01$). At this age however, group-reared rats are heavier than isolated animals. A significant difference in the same direction is present at the age of 6 months ($t = 3.7$, $p < .01$).

The results of various studies on the effects of isolated rearing on body weight are unequivocal. Hatch et al. (1963), working with an inbred strain of Wistar rats, reported significant lower body weights of individually caged rats in

comparison with those of group-reared animals. Animals were isolated or group-reared during a post-weaning period of 13 weeks. These data are in accordance with the present findings except for the non-significant differences at the age of 4 months in the present experiment. Gruendel and Arnold (1969) also found a significantly heavier weight in group-reared animals after a 70 day post-weaning isolation or group-reared period. Koch and Arnold (1972), working with albino rats and using a post-weaning period of 3 months, report that group-reared animals weighed significantly more than isolated animals at any age during the isolation period. The present findings are in accordance with data from studies by Latané et al., (1970). They found that in isolated animals at 70 days of age, following an isolation period of 40 days, a significantly heavier weight was observed in comparison with animals, which had been reared in groups of 6 for the same period. No difference existed between isolated animals and those reared in groups of 2 or 3 in a cage. Levitsky and Barnes (1972) did not find a significant difference in body weight between isolated and group-reared animals. Their isolated animals are slightly heavier after a 16 week isolation period and a reverse effect is seen after a 24 week isolation period. Van Woerden (in press) working with Tryon maze Bright rats, reports a significantly heavier weight in isolated animals in comparison with group-reared rats during a post-weaning period of 13 weeks. In a number of "enrichment" experiments, van Woerden was able to confirm differences found at younger ages in the present study. After a post-weaning period of isolation of one month, he consistently found the same result. Dolger (1955), using albino rats, also found a heavier weight in isolated animals after a post-weaning period of 70 days. Ward and Gerall (1968) working with Sprague Dawley rats, and Wilhelmsson and Larsson (1973) working with albino's reported a significantly heavier weight in isolated animals as compared with group-reared animals at 90 and 120 days respectively. They, however, weaned their animals very early, at the age of 10 and 14 days respectively. Korn and Moyer (1960) were unable to find a difference in body weight after an isolation period of 90 days. Singh and Maki (1968) reported an isolation study with albino rats in which a significantly heavier weight appeared for group-reared animals, after a one month post-weaning isolation or group-reared period.

The differences in results are obvious, but an explanation for these discrepancies seems to be difficult. Perhaps differences in rat strains used, time of

onset of isolation and housing conditions in the various studies, are responsible for the unequivocal results. On the other hand, the present findings suggest that different processes are at work during the period of isolation: a) a relatively short term effect of isolation which may be responsible for a rapid increase in initial body weight; b) long-term isolation, which probably results in a less rapid increase thereafter. However, long-term group-rearing under unstimulating laboratory housing conditions may also lead to a rapid increase in body weight beyond a certain age (e.g. 4 months). The explanations are hypothetical and need further investigation.

CONCLUSIVE REMARKS AND SUMMARY

The social behaviour of rats develops according to a predetermined plan, the realisation of which occurs in the interaction of the animals with their environment.

The young rat is born as a small helpless creature which is at first almost fully dependent upon the care of the mother. The mother is responsible for feeding, warmth, protection and she even initiates the processes of elimination. During the neonatal period (0-14 days) the mother takes the initiative in mother-young interaction. The neonatal pups, however, are able to produce ultrasonic signals to which the mother reacts with nest building and retrieval activities. With the exception of his contacts with mother and littermates, the interaction of the neonatal rat pup with the environment is very limited.

The development of behaviour during the neonatal period is characterized by the gradual completion of originally incomplete and fragmentary behaviour patterns, as well as the coupling of solitary elements or fragments into co-ordinated activities. The development of basal motor behaviour elements into rather complex behaviour patterns, seems to be under endogenic control, because it is synchronous with the development of the C.N.S. and the effector systems (Bronson 1964; p 41 to 47). Specific external stimulation seems to exert minor influence (Hinde, 1966). Specific stimulation during the neonatal period probably produces no specific effects, but exerts a diffuse influence on the development of emotional behaviour (Scott 1962; Denenberg 1964; Schneirla 1965; Hinde 1966). It is believed that the neonatal period is a sensitive period during which external stimulation directly influences the "chronical" or general arousal level, and indirectly influences the emotional behaviour of the animals at a later stage (Scott 1962, in a study on dogs). Quantitative aspects of external stimulation (intensity, time of exposure) seem to be especially important. Along with the development of visual and acoustic perception, qualitative aspects also become important. During the neonatal period sensoric information is produced primarily through olfaction and gustation and perhaps by the tactile sense.

Because of the limited motor behaviour development and behaviour repertoire, the reactions of the young animals are rather undifferentiated. Schneirla makes a distinction between approach and withdrawal activities as basic reactions during development of organisms. Early in ontogeny mild stimuli elicit approach behaviour whereas intense stimulation leads to withdrawal behaviour. During the neonatal period approach behaviour is primarily characterized by orientating responses (searching behaviour with the head, extension of forelimbs and/or forepart of the body) which eventually result in contact between stimulus and animal. Withdrawal activities may be regarded as those involving retraction of the head or forepart of the body, and the brief interruption of normal activities (Schneirla 1965; Bronson 1964; Small 1899; Welker 1964). Both types of behaviour result in a reduction of arousal and are reinforcing.

Repeated intensive stimulation resulting in a high level of reticular arousal, probably leads to adaptation to that level of arousal by raising the threshold for somatosensoric stimulation and to chronic decreased emotionality in the animal (Candland 1971; Schneirla 1965). The opening of the ears at about the 13th day and the opening of the eyes a few days later herald the beginning of important changes in the social behaviour of young rats. The animal is able to enjoy a more refined perception. Moreover, motor behaviour development and motor behaviour co-ordination are much more complete by now, and olfaction is almost adultlike. Gradually a shift can be observed in the initiative of the mother-young interaction. The young rats take the initiative in respect of feeding behaviour, while the importance of the role of the mother gradually decreases.

The young begin eating solid food. The young animals become more interested in other aspects of the environment besides mother and littermates. They explore everything in the environment and exhibit very active locomotory behaviour. The abundance of new sensoric and somato-sensoric stimulation increases the reticular arousal level which, at this stage, is not yet controlled by more rostral inhibitory centres, such as the hippocampus and neocortex, since these do not become functional before the 4th week after birth (p 41 to 47).

During the transition and the socialization periods (15-30 days), the behaviour repertoire is expanding very fast, and especially the elements of the social behaviour categories. At first, social behaviour elements are performed only fragmentarily, and a fixed sequence is absent in the series of fragments of behaviour ele-

ments. The elements alternate very rapidly and in an unpredictable manner. Behaviour performance seems to be under internal control and is apparently unrelated to specific characteristics of the environment, with the possible exception of eating. Often, behaviour elements belonging to the end of a sequence (consummatory activities) develop first whereas introductory activities (appetitive activities) develop later. The same phenomenon can be observed in other animal species as well (Tinbergen 1963). It is, however, remarkable that some assident aspects of behaviour elements characteristic of adult rat behaviour patterns are absent in young animals. In young rats, for instance, assident characteristics such as piloerection, biting and ultrasonic signalling are lacking as components of consummatory activities of the offensive agressive system (fighting and attacking). The absence of the secundary motivational characteristics, and the repeated performance of changing sequences of behaviour patterns, may be an indication that an aggressive motivation is not yet present during the transition and socialization periods, when young animals are involved with play behaviour. However, young rats belonging to these age groups are certainly able to perform in a completely adultlike fashion, as could be observed in rats of 30 days old which had been isolated for a week and then confronted with each other. Threatening activities were also absent in the normal hyperactive behaviour of group-reared young rats. The playful interactions between the animals consist of brief fragments of elements from the aggressive flight or fight systems. Some students assume that threatening activities develop out of separate fight or flight patterns and possess an ambivalent character. They are the expression of an internal conflict within the animal between the tendency to approach and the tendency to withdraw, or between the tendency to fight and the tendency to flight (Hinde 1972; Kruyt 1964).

Our own observation of animals from the transition and socialization periods lend further support to the theory of Schneirla concerning the development of behaviour in terms of approach and withdrawal reactions. Early in the transition period rather uninhibited exploratory behaviour was observed. The orientating responses prevalent during the neonatal period now pass into active exploratory activities. The development of the various senses create the possibility of directing attention actively. Every new stimulus is explored. The uninhibited tendency to explore

the environment also leads to intensive contact between littermates.
The reactions of withdrawal from new stimuli develop somewhat later and are presumably coincident with the development of feelings of fear and novelty.
Bronson (1964) has explained that the maturation of the C.N.S. is crucial for the development of fear of novelty, especially the maturation of the limbic system and the neocortex. The beginning of the appearance of reactions of fear is coincident with the termination of the sensitive period for the development of primary "attachment" (imprinting), and at the same time marks the beginning of the sensitive period for the development of integrated social behaviour (Scott 1962).
The process of primary attachment comes to an end at about day 21 and the sensitive period of socialization then begins. According to Scott, the process of socialization is one in which a gradual acquaintance with members of the same species is increasing, and thus resulting in reduction of fear. In our opinion the socialization period may be characterized as one in which the social behaviour of rats becomes stable and functional. The integration of different elements of the social behaviour repertoire into more complex behaviour patterns takes place during the playful interactions and the behaviour systems become harmoniously adjusted to each other.
There is poor balance between approach-withdraw behaviour, and concomitant fight-flight behaviour at the beginning of the socialization period (21-30 days), resulting in successive ambivalent behaviour. Normal group-reared animals do not perform simultaneous ambivalent behaviour. There is probably no motivational conflict in normal developing young rats. Such a conflict occurs under certain circumstances and it is then that we see behaviour patterns such as freezing, standing attention, sideways attack and threat. These elements were, for instance, observed in two young adult male rats, coming into a serious conflict with each other for the first time (p 65). Rats reared in isolation, however, often perform simultaneous ambivalent behaviour patterns during intraspecific aggressive interactions even at younger ages. The behaviour performance of isolated-reared rats has an unstable character and in contrast with the behaviour of normally developing young rats, a harmonious integration of separate elements does not exist. The interactions with littermates during a so called sensitive period are definitely important to the adaptive social development of the animals. For the rest the interaction with the mother is also important for a good social development. Gruendel and Arnold (1969) were able

to prove that both interaction with the mother and contact with littermates during the "play" period were necessary for the appearance of normal sexual behaviour in adult rats. Isolated reared rats are not able to adjust their behaviour to that of conspecifics, they react hyperemotionally and hyperaggressively. The increase in aggressive behaviour can be interpreted as stemming from the inability to react adequately to the behaviour of conspecifics. The hyperexcitability makes the animals extremely fearful of contacts with other rats, and hence they react hyperaggressively to approaches from others. The tendency to withdraw is neutralized by an equally strong tendency to approach. The animals are in a state of hyperarousal almost continuously. Supersensitivity of the noradrenaline receptors seems to be responsible for the heightened arousal. The supersensitivity is a result of the decreased rate of release of noradrenaline on the receptors as a consequence of isolated rearing. The beginning of the sensitive period for socialization coincides with the onset of the functioning of the telencephalic centres,known to play a role in inhibition of arousal and in regulation of behaviour. In particular, the hippocampus plays a major role (Moorcroft 1970). The process of socialization may be considered as a process of habituation to disturbing -non relevant- stimulation from conspecifics (Cairns and Nakelski 1971). Both the limbic system and the hippocampus are involved in the process of habituation (Vossen 1969). It seems valid to assume that the disturbed overt behaviour of isolated rats stems from non-functioning inhibiting structures, which prevent the animals from adjusting appropriately to their environment. Rats reared in social isolation are perhaps not able to respond selectively to environmental stimulation, and to make a distinction between biologically relevant and irrelevant stimuli.

Carlton considers habituation to be a process of filtering; animals respond to biologically relevant and not to irrelevant stimulation. The cholinergic inhibitory system plays a major role in this process (Vossen 1969). The findings of Melzack (1969) in isolated reared dogs are in agreement with the assumptions presented above. Melzack, observing the behaviour of socially isolated dogs, which is in essence identical to that of isolated rats, draws the conclusion that the total input bombarding the C.N.S results in excessive arousal, because the animals are not able to (learn to) filter out irrelevant information. Neuropharmacological research in rats point in the same direction. Isolated rats possess a lower amount of acetyl

choline -the neurotransmitter present in cholinergic inhibitory circuits- and this results in decreased cholinergic transmission (Valzelli 1973). There exists a strong coherence between environmental stimulation and maturation processes occurring within the C.N.S. The absence of environmental stimulation results in certain brain centres not becoming functional, and thus in disturbance of overt behaviour.

The socialization period is one in which rats learn to adjust their behaviour to that of conspecifics through intensive interaction. A harmonious integration of behaviour elements into behaviour systems also takes place within this period. In isolated animals both hyperarousal and non-functioning of inhibiting structures of the C.N.S. occurs. The resulting aggressive behaviour observed in isolated animals is a mixture of "fear-induced" and "irritable" aggression (Moyer 1966). Our study indicated that a short isolation period which ends before the conclusion of the play period, brings about reversible disturbances of behaviour, whereas long isolation periods cause irreversible disturbances. Possibly the whole "play" period is the sensitive one to the development of adequate social behaviour, as Scott (1962) has concluded from his studies on puppies.

During the juvenile period (30-60 days) the behaviour gradually loses a playful character and acquires the characteristics of adult performance. According to Scott (1962) the end of the play period also marks the end of the period critical for the learning of normal social behaviour. We have not examined to what extent this suggestion holds true. It became clear that during the juvenile period the role differentiation between male and female rats gradually developed. The males became responsible for almost the total observed frequency and total time of aggressive behaviour and male sexual behaviour. Play behaviour, still frequently present at the beginning of the juvenile period, gradually decreases while the more complete and co-ordinated performance is developing.

Activities seem to occur in the correct motivational context and as appropriate reactions to eliciting stimuli. The method of observation we used was not sufficiently refined to trace this development in greater detail.

The young rats, especially the males, loose their immunity now: the adult male rats and lactating females encounter them aggressively. This change occurs between about the 50th and 60th day and may coincide with the attainment of sexual maturity

by the young subadults. Among wild rats the increasing aggressive character of the encounters between male adults and young male rats results in dispersion of the young males during the subadult period. The various behaviour elements from the social behaviour repertoire integrate into the recognizable adult sequences and the distinct behaviour systems become adjusted to each other harmoniously.
The rats of the subadult period (60-90 days) possess almost all the characteristics observable in the behaviour of adult animals. They perform the separate patterns and postures in their complete forms, distinct elements have a longer time of performance and abrupt and unexpected transitions between elements are absent. The animals spend much time in non-social activities such as exploration and grooming within the subadult period. The adult behaviour sequences now present are an indication of the completed spatiotemporal organization of behaviour. The fixed species-specific sequences occur as reactions to particular stimuli, dependent on the internal physiological state of the animal. In sexual behaviour for instance, the distinct elements are performed in the adult temporal sequence and the sequence is continued up to and including the last element. Female rats deliver their first offspring close to the end of the subadult period.
Heavy fights occurred between male rats -littermates- for the first time at about the 90th day. The aggressivity between the males was interpreted to have a function in acquiring an individual territory. Adult animals reacting very aggressively to subadult animals cause them to disperse under natural conditions (Barnett 1963; Ewer 1967; Calhoun 1962). In our study, the seminatural environment prevented the dispersion of the subadult males. The territorial aggression observed, resulted in the death of two male animals and the survival of one male in each litter. Various students assume that rats establish individual territories (Steiniger 1950; Galeff 1970; Barnett 1964). Steiniger (1950) assumes that a rat pair establishes a so called "Rudel" within a certain region. Intruders are expelled from the region, male intruders by the male parent and the female intruders by the mother rat. Steiniger, however, makes no mention of intragroup aggression. We did not observe aggressive behaviour between the females which could eventually result in the survival of one female rat. There were, however, indications that in one litter only one female was responsible for procreation and for newborn rats, and this was observed over a long period until the time the surviving male and the original three female litter-

mates had reached an age of 11 months. In this litter, lethal fights broke out between the father abd his sons as soon as these had reached an age of between 3 and 4 months. The result was also interpreted as due to the obstruction of the dispersion of the young males, which eventually would, under normal circumstances, lead to the acquisition of an individual territory. The fights led to the subsequent death of the young adults. No fights between group-reared rats occurred in the study concerning the effects of social isolation on aggression, not even in groups which lived together for 6 months. The housing of the animals within a small cage possibly opposes the process of establishing an individual territory (Galeff 1970). It cannot be excluded from consideration however, that the absence of female rats inhibits the production of androgens in male animals. Androgens are known to play a role in the production of a pheromone which functions as both aggression eliciting and aggression inducing in male mice (Mugford and Nowell 1970, 1971). Before being able to draw valid conclusions, we must explore to what extent tne male rats' sexual maturation, resulting in the secretion of androgenic substances, lingers as a consequence of the absence of female rats.

Timmermans (1977), however, has confirmed our observation. No fights occurred in groups of rats which had been composed even heterogeneously, neither in groups of T.M.D. rats, housed in small macrolon cages, nor in wild rats, housed in a small environment (2 m^2). It is possible that rats need a minimal area in order to develop territorial aggression within a group of rats familiar to each other. Further research is needed, for instance to develop a suitable standard test situation which can be used in various investigations concerning the study of territorial aggression in rats. The enormous diversity in rearing conditions, test situations and methods of research is obstructive to drawing valid conclusions in comparing research findings. In any case, the test environment we used in our study seems less suitable for research of territorial aggression in rats.

SLOTOPMERKINGEN EN SAMENVATTING

De ontwikkeling van het sociale gedrag van de rat verloopt volgens een bepaald "plan" dat tot verwerkelijking komt in de interaktie van het dier met de omgeving waarin het opgroeit.
De jonge rat wordt geboren als een hulpeloos wezen dat voor zijn ontwikkeling in eerste instantie vrijwel volledig afhankelijk is van de zorgen van de moeder. De moeder draagt zorg voor voeding, warmte, bescherming en brengt zelfs de processen van uitscheiding bij de jongen op gang. Gedurende de eerste 14 dagen gaat vrijwel alle initiatief in de moeder-jong interaktie van de moeder uit. De jonge ratten brengen wel geluiden voort, waarop de moeder reageert met nestbouw en retrieval gedrag en zorg draagt voor verwarming van de jongen door op het nest te blijven. De gedragsmatige interaktie van de jonge rat met zijn omgeving is dan nog zeer beperkt. Er is slechts sprake van vrijwel voortdurend kontakt met de moeder, die het overgrote gedeelte van de tijd bij de jongen in het nest verblijft, en van diffuus taktiel kontakt met de nestgenoten.
Wat de ontwikkeling van het gedrag betreft wordt de neonatale periode (0-15 dagen) vooral gekenmerkt door de vervolmaking van oorspronkelijk vaak onvolledige of fragmentarische gedragspatronen of de samenkoppeling van afzonderlijke elementen of delen van elementen tot gecoördineerde handelingen. De ontwikkeling van de basale motorische bouwelementen naar meer complexe handelingen lijkt vooral endogeen bepaald te zijn en samen te vallen met de ontwikkeling van het centrale zenuwstelsel en de effector systemen (Bronson 1964; p 32 t/m 36). De ontwikkeling lijkt weinig beïnvloedbaar door specifieke externe stimulatie (Hinde 1966).
De indruk bestaat dat specifieke stimulatie in deze periode geen specifieke effekten met zich meebrengt, maar dat elke vorm van stimulatie een diffuus effekt heeft in die zin dat toekomstig emotioneel gedrag in sterkte gereduceerd wordt (Scott 1962; Denenberg 1964; Schneirla 1965; Hinde 1966). De neonatale periode wordt derhalve geacht een zgn. sensitieve periode te zijn, waarbij externe stimulatie direkt het "chronische" of algemene arousal niveau beïnvloedt en indirect -via deze beïnvloeding- het latere emotionele reageren van de dieren(Scott 1962 in onderzoek bij honden). Het zijn vooral de kwantitatieve aspekten van de externe stimulatie (intensiteit, duur) die van belang zijn. Pas met de ontwikkeling

van de visuele en acoustische perceptie worden kwalitatieve aspekten belangrijk (Denenberg 1964; Schneirla 1965). In de neonatale periode vindt sensorische informatie vooral via de reuk en smaak en mogelijk taktiel plaats.
Aangezien de motorische mogelijkheden en het gedragsrepertoire als geheel nog zeer beperkt zijn, zijn ook de reaktiewijzen weinig gedifferentieerd. Schneirla maakt onderscheid tussen naderings- en terugtrekreakties als basisreakties in de ontwikkeling van organismen. In de vroege ontwikkeling lokken milde stimuli naderingsgedrag uit, terwijl intensieve stimuli tot terugtrekgedragingen leiden. Het naderingsgedrag heeft in de neonatale periode vooral het karakter van oriëntatiereakties (zoekbewegingen met het hoofd, extensie van voorkant) die eventueel leiden tot kontakt. Terugtrekgedragingen zijn bijvoorbeeld het afwenden of terugtrekken van het hoofd of het gedurende korte tijd onderbreken van aktiviteiten Schneirla 1965; Bronson 1964; Small 1899; Welker 1964). Beide vormen van gedrag leiden totverlaging van arousal en zijn "belonend". Herhaalde intensieve stimulatie die een hoog niveau van reticulaire arousal tot gevolg heeft, leidt waarschijnlijk tot adaptatie aan dat niveau door verhoging van de drempelwaarde t.a.v. somatosensorische stimulatie en tot blijvend lagere emotionaliteit van het dier (Candland 1971; Schneirla 1965).
Het openen van de oren omstreeks de 13e dag en het openen van de ogen enkele dagen later leiden een belangrijke verandering in in het sociale gedrag van de jonge rat. Het dier is in staat tot een betere waarneming. Bovendien is op dit tijdstip de motorische ontwikkeling en coördinatie bijna volledig en funktioneert het reukorgaan op de volwassen manier.
Geleidelijk vindt nu ook een opmerkelijke verandering plaats in de moeder-jong interaktie. Het initiatief tot voedingskontakten gaat steeds meer van de jongen uit en steeds minder van de moeder. Ook gaan de jongen nu vast voedsel eten.
De dieren zijn meer mobiel en krijgen meer belangstelling voor de aspekten van de omgeving buiten de moeder en de nestgenoten. Ze exploreren en besnuffelen alles en vertonen als gevolg hiervan een sterke mate van locomotie. De overvloed aan nieuwe sensorische en somato-sensorische stimulatie verhoogt het reticulair arousal niveau dat nog niet onder kontrole staat van meer rostraal gelegen inhiberende gebieden als de hippocampus en de neocortex, die eerst funktioneel worden

in de 4e week na de geboorte (p 45 en 46).
In de transitie en de socialisatieperiode (15-30 dagen) breidt het gedragsrepertoire zich zeer snel uit. Vooral de elementen uit het sociale gedragsrepertoire ontwikkelen zich nu. In eerste instantie worden de sociale gedragingen veelal slechts fragmentarisch uitgevoerd en is er geen enkele vaste volgorde in de reeks brokstukken van gedragselementen te ontdekken. De elementen wisselen elkaar zeer snel af. Het gedrag in deze periode lijkt vooral onder interne kontrole te staan en is niet of nauwelijks afgestemd op specifieke kenmerken van de omgeving. Een uitzondering vormt het eetgedrag. Het komt vaak voor dat eindgedragingen -consummatory activities- zich eerst ontwikkelen, en daarna pas de inleidende gedragingen -appetitive activities- tot ontwikkeling komen. Op zichzelf is dat geen bijzonder verschijnsel, het komt ook bij andere diersoorten dan de rat voor (Tinbergen 1963). Opmerkelijk is wel dat bij een aantal van de eindgedragingen sekundaire kenmerken zoals die bij volwassen dieren waargenomen kunnen worden, ontbreken. Zo ontbreken bij de jonge dieren bij de consummatoire aktiviteiten van het offensieve agressieve systeem (vechten, bespringen) bijbehorende kenmerken als piloerektie, bijten, ultrasone geluiden etc. De afwezigheid van sekundaire motivationele kenmerken en het herhaaldelijk optreden van grillige gedragssequenties doen vermoeden, dat er in deze fase bij ratten in hun spelgedrag nog geen sprake is van een agressieve motivatie. Dat jonge ratten overigens wel in staat zijn die kenmerken te vertonen blijkt uit het vechtgedrag van ratten van 30 dagen die een tijdlang geïsoleerd zijn opgegroeid en met elkaar gekonfronteerd worden. Bij deze geïsoleerd opgegroeide dieren konden herhaaldelijk tijdens het vechten sekundaire motivationele kenmerken worden waargenomen. In het normale hyperaktieve gedrag van jonge ratten ontbreken ook de zgn. dreiggedragingen. De spelinterakties tussen de dieren bestaan vooral uit kortdurende fragmenten van gedragselementen uit het agressieve aanvals- en vluchtsysteem. Sommige auteurs veronderstellen dat de dreiggedragingen zich ontwikkelen uit de afzonderlijke aanvals- en vluchtelementen; dientengevolge hebben deze gedragingen een ambivalent karakter. Ze zijn uitingen van een in het dier aanwezig konflikt tussen de neiging te naderen en de neiging weg te lopen, c.q. aan te vallen of te vluchten (Hinde 1972; Kruyt 1964).

De eigen waarneming bij dieren in de transitie en socialisatieperiode geven verdere grond aan de opvatting van Schneirla betreffende de ontwikkeling van gedrag in termen van naderings- en terugtrekreakties. In eerste instantie is er in de transitieperiode vooral sprake van ongeremd exploratief gedrag. De oriëntatiereakties uit de neonatale periode gaan over in aktieve exploratie. Door de ontwikkeling van de verschillende zintuigmodaliteiten wordt de mogelijkheid geschapen de aandacht aktief te richten. Elke nieuwe stimulus wordt geëxploreerd. Ook het eerste aktieve kontakt met de nestgenoten komt voort uit de ongeremde exploratiedrang.

De terugtrekreakties op nieuwe stimuli komen iets later tot stand en hangen waarschijnlijk samen met de ontwikkeling van gevoelens van angst voor nieuwheid. Bronson (1964) heeft erop gewezen dat de verdere rijping van het C.N.S. bepalend is voor deze ontwikkeling, en wel met name de ontwikkeling van het limbische systeem en van de neocortex. Het begin van de angstreakties valt volgens Scott (1962) samen met het eindpunt van de sensitieve periode voor de ontwikkeling van primaire "attachment" (imprinting) en is tevens het begin van de sensitieve periode voor de ontwikkeling van geïntegreerd sociaal gedrag. Het proces van primaire attachment eindigt rond de 21e dag; rond die tijd begint de sensitieve periode voor socialisatie. Het proces van socialisatie is volgens Scott een proces van toenemende bekendheid met de soortgenoten die angstreducerend werkt. Ons inziens is de socialisatieperiode de periode waarin het sociale gedrag van de dieren stabiliteit verwerft en doelmatig wordt. Tijdens de spelaktiviteiten vindt de integratie van verschillende elementen van het sociale gedrag tot komplexere gehelen plaats en worden de gedragssystemen harmonisch op elkaar afgestemd.

Aan het begin van de socialisatieperiode (21-30 dagen) is er sprake van een slechte balans tussen naderings- terugtrek, resp. aanvals- en vluchtgedragingen, hetgeen tot uiting komt in successief ambivalent gedrag. Van simultaan ambivalent gedrag is bij normale dieren geen sprake. Waarschijnlijk is er bij normaal opgroeiende ratten geen sprake van een motivationeel konflikt. Pas in een situatie waarin zo'n konflikt wel aan de orde is, zien we gedragingen als freezing, staand afweren, zijwaarts aanvallen, dreigen, zoals bij de jong volwassen mannelijke ratten die voor het eerst in hun ontwikkeling in een serieus gevecht raakten (p 64). Geïsoleerde dieren vertonen deze ambivalente gedragingen daarentegen ook op jonge leeftijd

frekwent tijdens intraspecifieke agressieve interakties. In tegenstelling tot de waarnemingen bij normaal opgroeiende jonge ratten, blijft het gedrag van geïsoleerd opgegroeide ratten instabiel en is er van harmonische integratie van afzonderlijke elementen geen sprake. De interakties met leeftijdsgenoten gedurende een daarvoor gevoelige periode zijn kennelijk belangrijk voor de adaptieve sociale ontwikkeling van de dieren.Overigens is ook de interaktie met de moeder van belang voor een goede sociale ontwikkeling. Gruendel en Arnold (1969) toonden aan dat voor het verschijnen van normaal sexueel gedrag bij volwassen ratten, zowel interaktie met de moeder als kontakt met leeftijdsgenoten gedurende de "spel"-fase belangrijk waren. Timmermans (1977) toonde echter aan dat ook streng geïsoleerde dieren (met de hand opgevoed) in staat waren tijdens de eerste bronstperiode waarin mannetjes-en vrouwtjesratten samen waren, nageslacht te verwekken en resp. te krijgen ondanks gestoord sexueel gedrag. De stoornissen (verkeerde oriëntatie, onjuiste gedragssekwenties) waren kennelijk niet blijvend maar van tijdelijke aard en reversibel.

Geïsoleerde ratten zijn niet in staat hun gedrag af te stemmen op het gedrag van soortgenoten. Ze reageren hyperemotioneel en hyperagressief. De toename in agressief gedrag valt te duiden als direkt voortvloeiende uit het onvermogen adekwaat te reageren op het gedrag van soortgenoten. De hyperexcitabiliteit maakt de dieren extreem angstig in de kontakten en geeft hun reakties eem uiterst agressief karakter. De neiging tot terugtrekgedrag wordt genivelleerd door een even sterke neiging tot naderingsgedrag. De dieren verkeren in een voortdurende toestand van hyperarousal. De verhoogde arousal blijkt een gevolg te zijn van supersensitiviteit van noradrenaline receptoren. Deze verhoogde gevoeligheid is een gevolg van een vertraagde mate van release van noradrenaline met als gevolg een overgevoeligheid van de receptoren ten gevolge van isolatie. Het begin van de sensitieve periode voor het leren van sociaal gedrag valt samen met het functioneel worden van telencephale centra die te maken hebben met inhibitie van arousal en de regulering van gedrag. Met name de hippocampus speelt daarbij een rol (Moorcroft 1970).Socialisatie kan opgevat worden als een proces van habituatie aan verstorende -niet relevante- stimulatie van soortgenoten (Cairns en Nakelski 1971). In het proces van de totstandkoming van habituatie speelt het limbische systeem en de hippocampus een belangrijke rol (Vossen 1969). De veronderstelling lijkt gewettigd dat de verstoring in het overte gedrag van geïsoleerde ratten een gevolg is van het niet funktioneel worden van gedragsinhiberende strukturen, waardoor de dieren niet in

staat zijn hun gedrag adekwaat af te stemmen op de omgeving. Sociaal geïsoleerde dieren zijn wellicht niet in staat te leren een selektie toe te passen op omgevingsstimulatie en onderscheid te maken tussen biologisch relevante en biologisch niet relevante stimulatie. Volgens Carlton kan habituatie beschreven worden in termen van een proces van filtering, waarbij wel gereageerd wordt op biologisch relevante prikkels, maar niet op biologisch niet-relevante. Het cholinerge inhibitiesysteem (met o.a. hippocampus) speelt daarbij een belangrijke rol (Vossen 1969).

In overeenstemming met deze opvatting zijn de bevindingen van Melzack (1969) bij geïsoleerd opgegroeide honden. Melzack trekt uit de observaties van het gedrag van de geïsoleerde dieren, dat in veel opzichten identiek is aan het gedrag dat wij bij geïsoleerde ratten observeerden, de konklusie dat de totale input die het centrale zenuwstelsel bombardeert, tot de excessieve arousal leidt omdat de dieren niet in staat zijn (niet kunnen leren) irrelevante informatie uit te filteren. Neuropharmacologisch onderzoek bij ratten wijst in dezelfde richting. Acetylcholine -de neurotransmitter in cholinerge inhibitiecircuits- is minder aanwezig in geïsoleerd opgegroeide dieren en dit leidt tot verslechtering van cholinerge transmissie (Valzelli 1973). Tussen ervarings- of omgevingsinvloeden en rijpingsprocessen die plaats vinden in het C.N.S. blijkt een zeer sterke samenhang te bestaan. Het ontbreken van bepaalde omgevingsinvloeden leidt tot het niet funktioneel worden van bepaalde hersencentra en dat leidt weer tot verstoring van het overte gedrag.

Onze konklusie is dat de socialisatieperiode een periode is waarin de dieren middels het kontakt met soortgenoten leren hun gedrag af te stemmen op die soortgenoten en waarin een harmonische integratie van de gedragselementen tot gedragssystemen plaatsvindt. Isolatie gedurende deze periode leidt tot onaangepast gedrag. Bij de geïsoleerde dieren is er sprake zowel van hyperarousal als van een verstoring van het funktioneel worden van inhibitiestrukturen in het C.N.S. De waargenomen vorm van agressie bij de geïsoleerde dieren kan beschreven worden als een mengeling van "fear-induced" en "irritable" aggression (Moyer 1966).
Er zijn aanwijzingen dat een korte isolatieperiode, die eindigt voor het einde van de spelperiode, reversibele gedragsstoornissen teweeg brengt. Langdurige isolatie leidt tot meer irreversibele stoornissen. Mogelijk vormt de gehele spelfase de sensitieve periode voor het ontwikkelen van aangepast sociaal gedrag. Deze opvatting is in overeenstemming met die van Scott (1962) in onderzoek met puppies. Gedurende de juveniele periode (30-60 dagen) verliest het gedrag geleidelijk zijn spelkarakter en vertoont het steeds meer de kenmerken van volwassen gedrag. Volgens

Scott (1962) valt het einde van de spelperiode samen met het einde van de sensitieve periode voor het leren van normaal volwassen sociaal gedrag. In hoeverre deze suggestie juist is, is in de onderhavige studie niet onderzocht. Duidelijk werd in elk geval dat de differentiatie tussen mannelijke en vrouwelijke dieren, tot uitdrukking komend in gedrag, in deze periode gestalte begint te krijgen.
De mannelijke dieren blijken in toenemende mate verantwoordelijk voor de waargenomen totale frekwentie van voorkomen van agressief gedrag (offensief en defensief) en paargedrag (bestijgen en pogingen tot bestijgen). Het in het begin van de juveniele periode nog zeer frekwent aanwezig spelgedrag, wordt minder frekwent naarmate het gedrag volledíger en gekoördineerder wordt uitgevoerd en de handelingen tussen de dieren steeds meer op elkaar worden afgestemd. De handelingen lijken nu te verschijnen in de juiste motivationele kontext en in de aanwezigheid van de juiste uitlokkende stimuli. Onze methode van onderzoek was niet verfijnd genoeg om deze ontwikkeling nauwkeurig te beschrijven.
De jonge -vooral mannelijk- dieren verliezen nu ook hun immuniteit: ze worden door volwassen mannelijke dieren en de lacterende vrouwelijke dieren soms agressief benaderd. Deze omwenteling vindt plaats rond de 50 à 60e levensdag en zou samen kunnen hangen met het bereiken van sexuele rijpheid van de mannelijke dieren rond die tijd. Bij wilde ratten leidt de steeds toenemende agressiviteit van volwassen dieren tegen de jonge mannelijke dieren tot de verwijdering van deze jonge dieren in de loop van de subadulte periode.
De verschillende elementen uit het sociale repertoire integreren tot de herkenbare volwassen gedragssekwenties en de verschillende gedragssystemen worden harmonisch op elkaar afgestemd.
De rat in de subadulte periode (60-90 dagen) bezit nagenoeg alle gedragskenmerken die waargenomen kunnen worden bij volwassen dieren. De afzonderlijke gedragingen worden volledig uitgevoerd, duren gemiddeld langer en onlogische of abrupte overgangen tussen gedragselementen komen nog slechts zelden voor. Erg veel tijd besteden de dieren in deze periode aan niet-sociale gedragingen als exploratie en poetsgedrag. De thans optredende volwassen gedragssekwenties duiden op een voltooide spatiotemporale organisatie van het gedrag.
De soorttypische gedragssekwenties treden op als reaktie op bepaalde prikkels, afhankelijk van de interne fysiologische toestand van het dier. Een voorbeeld hiervan vormt het sexuele gedrag: de onderscheiden gedragselementen beginnen in deze periode in de juiste temporele volgorde op te treden; de volgorde wordt tot het

eindgedrag volgehouden.
Tegen het einde van de periode, omstreeks de 90e levensdag, krijgen rattenvrouwtjes hun eerste jongen.
Omstreeks de 90e dag breken tussen de mannelijke dieren -nestgenoten- ook de eerste serieuze gevechten uit. Deze vijandigheid tussen de mannelijke dieren kan naar onze mening uitgelegd worden als agressie in dienst van het verwerven van een individueel territorium. Onder natuurlijke omstandigheden vindt normaliter dispersie plaats van de subadulte dieren, veelal veroorzaakt of uitgelokt door sterk agressief gedrag van volwassen dieren tegenover de subadulte mannelijke ratten (Barnett 1963; Ewer 1967; Calhoun 1962). De mogelijkheid tot dispersie was in de huidige seminatuurlijke omgeving niet aanwezig. De waargenomen territoriale agressie leidde in alle nesten tot de dood van twee mannelijke dieren en het overleven van één dier. Volgens sommige auteurs vestigen ratten inderdaad individuele territoria (Steiniger 1950; Calhoun 1962; Galeff 1970; Barnett 1964). Steiniger (1950) veronderstelt dat een rattenpaar in een bepaald gebied een zgn. Rudel vestigt. Indringers worden uit dat gebied verdreven, de mennelijke indringers door het mannelijke ouderdier en de vrouwelijke indringsters door de moeder. Hij vermeldt niet dat er binnen de Rudel intragroup agressie optrad, zoals wij waar konden nemen. In ons onderzoek werd geen agressief gedrag tussen de vrouwtjes onderling in de nesten waargenomen, dat eventueel zou kunnen leiden tot het overblijven van een vrouwtje. Bij het ene nest, waarbij dat enigszins systematisch gevolgd werd, leek het er overigens wel op dat slechts één vrouwtje zorg droeg voor de voortplanting en zorg voor de jongen.
Eén nest werd in zijn ontwikkeling gevolgd tot het tijdstip waarop het enig overlevend mannelijke dier en de drie oorspronkelijke vrouwelijke nestgenoten een leeftijd hadden bereikt van 11 maanden. In overeenstemming met de uitleg die we gaven aan de territoriale agressie en het dispersiefenomeen, braken tussen de vader en zijn zonen -lethale- gevechten uit, zodra de jongen tussen 3 en 4 maanden oud waren. De gevechten leidden tot de systematische uitroeiïng van de jong volwassen mannelijke dieren.
In het onderzoek naar effekten van isolatie op agressief gedrag braken tussen de in groepen opgroeiende dieren geen gevechten uit, zelfs niet bij die ratten welke gedurende 6 maanden samen opgroeiden. De mogelijkheid bestaat dat huisvesting in een kleine ruimte de ontwikkeling van individule territoria in de weg staat (Galeff 1970). Niet uitgesloten kan worden dat de afwezigheid van vrouwtjes de pro-

duktie van androgene stoffen in mannelijke dieren remt. Het is bijv. bij mannelijke muizen bekend dat de produktie van een geurstof die zowel agressie uitlokkend als agressie inducerend werkt, en afgescheiden wordt via de preputiaalklieren, androgeen bepaald wordt (Mugford en Nowell 1970, 1971). In hoeverre de geslachtelijke ontwikkeling die zou leiden tot afscheiden van androgene stoffen achterblijft tengevolge van de afwezigheid van vrouwtjes dient dan nader onderzochte te worden. Overigens heeft bijv. Timmermans (1977) de waarneming van ons kunnen bevestigen. In kleine, zelfs naar sexe heterogeen samengestelde groepen ratten,braken geen gevechten uit,noch bij in kleine macrolonkooien gehuisveste dieren (T.M.D ratten), noch bij in kleine omgevingen (2 m^2) gehuisveste dieren (wilde ratten). Wellicht is er toch een minimale oppervlakte noodzakelijk om ratten in staat te stellen in een groep elkaar bekende ratten territoriale agressie te gaan vertonen. Nader onderzoek op dit punt lijkt gewenst. Met name kan dan uitsluitsel verkregen worden ten aanzien van bijv. een goede standaard testsituatie die te gebruiken valt bij allerlei onderzoek naar beïnvloeding van territoriaal agressief gedrag van ratten. De huidige stand van zaken die gekenmerkt wordt door diversiteit in opgroeikondities, testsituaties en methodes van onderzoek, maakt een zinnige vergelijking van resultaten welhaast onmogelijk. De testomgeving die we gebruikten ter bestudering van agressief gedrag (p ^{79}) lijkt in elk geval minder geschikt om onderzoek te doen naar territoriaal agressief gedrag bij de rat.

TABELLEN EN FIGUREN

BEHORENDE BIJ

HOOFDSTUK II

	Age (months)							Age (months)					
	1	2	3	4	5	6		1	2	3	4	5	6
Approach	9.5	4.8	4.4	6.0	4.0	10.0	Evade	26.7	14.5	11.2	14.7	9.5	13.1
Attend	54.7	39.9	38.8	40.6	23.0	29.6	Retreat	5.4	3.2	1.4	1.7	1.2	2.2
Follow	8.3	3.5	3.5	3.3	1.1	3.6	Withdraw	4.3	2.0	3.8	2.2	1.1	0.6
Investigate	68.1	69.6	73.9	74.9	54.4	86.6	Flee	0.5	0.0	0.6	0.0	0.4	0.2
Nosing	0.0	1.2	0.2	0.0	0.8	4.0	Freezing	1.4	14.6	18.2	0.0	29.8	0.0
Oral inspection	0.2	0.0	0.6	0.0	0.2	1.0	Keep off lying	49.1	14.3	9.1	2.8	2.7	0.8
Anogenital insp.	9.1	9.9	4.4	3.1	5.1	1.8	Squirm	3.9	0.5	0.0	0.1	1.1	0.0
Crawl under	0.8	1.6	0.4	1.2	0.4	1.5	Fall sidew.or backw.	11.4	4.3	1.2	1.2	0.2	0.3
Social grooming	0.0	0.2	0.2	0.0	0.0	3.8	Full subm.post.	46.3	21.3	11.1	1.6	0.9	0.0
Aggressive grooming	1.2	1.2	0.1	0.1	0.0	0.2	Kick	3.6	2.4	0.2	0.6	0.0	1.6
Crawl across	1.6	0.8	0.9	0.9	0.1	0.6	Sidew.defens.post.	23.8	9.9	6.8	7.1	3.6	4.8
Touch	13.8	12.8	8.3	8.2	3.7	7.8	Sitting defens.post.	0.8	4.3	2.4	1.3	2.7	2.4
Take hold	12.0	8.2	4.7	5.1	2.2	2.1	Shrink back	0.4	0.2	0.4	0.2	0.4	0.3
Hold fast	15.3	10.0	20.2	1.1	3.7	2.7	Box	0.4	0.0	0.0	0.0	0.0	0.0
Dash	0.0	0.0	0.0	0.0	0.0	0.0	Upright	30.8	5.7	6.4	2.4	1.0	0.9
Mount	0.0	0.5	0.8	0.1	0.1	0.0	Standing attention	0.0	0.4	4.3	0.0	2.0	0.7
Present passively	0.0	0.0	0.1	0.0	0.7	0.0	Parry	19.6	27.0	45.9	11.4	19.6	7.1
Push	0.0	0.0	0.0	0.0	0.0	0.0	Exploration	180.0	268.5	206.8	357.7	296.2	354.5
Push aside	0.9	0.0	0.1	0.6	1.0	0.2	Stretched attention	2.7	6.0	5.9	7.7	6.8	8.0
Strike	5.8	2.4	1.3	1.2	0.4	2.5	Rocking	0.0	0.0	0.0	0.0	0.0	0.2
Pull	0.4	0.0	0.0	0.0	0.0	0.0	Sit	147.0	166.9	201.6	112.5	272.3	146.9
Snap	0.0	0.0	0.0	0.0	0.0	0.0	Rest	0.0	0.0	0.4	0.0	0.0	0.0
Bend over	0.0	0.0	0.0	0.0	0.0	0.1	Locomotion	20.7	12.8	13.5	18.8	12.8	21.1
Threat	4.4	1.6	2.4	2.6	3.9	4.2	Dally	0.7	0.0	0.0	0.0	0.0	0.0
Impress	0.0	0.0	0.0	0.0	0.0	0.0	Jump	0.0	0.0	0.0	0.0	0.0	0.0
Sideways attack	0.7	2.7	3.1	0.4	0.7	1.8	Dig	0.2	0.2	0.3	1.1	0.2	4.2
Lunge	0.0	0.0	0.5	0.0	0.3	0.0	Throw up	0.0	0.0	0.0	0.0	0.0	0.0
Fight	14.8	33.2	13.6	11.8	15.2	8.8	Eat	0.0	0.7	3.8	6.4	2.0	1.4
Bite	4.6	0.7	0.2	1.0	2.3	0.3	Drink	0.0	0.4	0.0	0.0	0.0	0.0
Push over and backw.	10.1	4.3	1.1	0.5	0.1	0.3	Groom	8.8	86.3	59.5	64.1	38.2	53.6
Keep down	75.2	23.1	10.2	0.9	2.2	0.1	Lick wounds	0.0	0.0	90.9	120.7	69.2	102.1
Chase	0.0	0.0	0.3	0.0	0.3	0.0	Tail rattle	0.0	1.3	0.0	0.0	0.0	0.0

Table 2. Mean total time (seconds) spent on different activities per observation session by the I-I animals.

	Age (months)					
	1	2	3	4	5	6
Approach	8.8	4.8	4.2	6.0	3.9	9.3
Attend	54.5	39.7	36.5	40.2	22.9	29.3
Follow	6.0	3.0	2.5	2.9	1.0	2.9
Investigate	30.6	26.1	25.3	37.3	20.1	37.8
Nosing	0.0	0.8	0.2	0.0	0.4	2.4
Oral inspection	0.2	0.0	0.2	0.0	0.2	0.6
Anogenital insp.	3.6	3.8	2.6	1.5	2.4	1.0
Crawl under	0.8	1.6	0.4	1.2	0.4	1.2
Social grooming	0.0	0.1	0.1	0.0	0.0	1.1
Aggressive grooming	0.6	0.7	0.1	0.1	0.0	0.1
Crawl across	1.6	0.8	0.9	0.9	0.1	0.5
Touch	13.8	10.5	8.2	8.2	3.7	7.1
Take hold	11.5	8.0	4.6	5.1	2.2	1.5
Hold fast	6.9	4.4	1.8	0.9	1.0	1.4
Dash	0.0	0.0	0.0	0.0	0.0	0.0
Mount	0.0	0.3	0.6	0.1	0.1	0.0
Present passively	0.0	0.0	0.1	0.0	0.1	0.0
Push	0.0	0.0	0.0	0.0	0.0	0.0
Push aside	0.9	0.0	0.1	0.5	0.2	0.1
Strike	4.3	1.7	1.3	1.2	0.3	1.3
Pull	0.2	0.0	0.0	0.0	0.0	0.0
Snap	0.0	0.0	0.0	0.0	0.0	0.0
Bend over	0.0	0.0	0.0	0.0	0.0	0.0
Threat	2.4	0.7	1.4	1.1	1.4	1.4
Impress	0.0	0.0	0.0	0.0	0.0	0.0
Sideways attack	0.4	1.0	1.6	0.2	0.5	0.6
Lunge	0.0	0.0	0.2	0.0	0.1	0.0
Fight	3.8	4.2	1.8	1.0	2.8	1.6
Bite	2.9	0.4	0.2	0.4	0.7	0.3
Push over and backw.	10.0	2.8	1.1	0.5	0.1	0.3
Keep down	8.8	1.7	0.9	0.4	0.7	0.1
Chase	0.0	0.0	0.2	0.0	0.2	0.0

	Age (months)					
	1	2	3	4	5	6
Evade	25.8	14.4	11.2	14.7	9.5	12.8
Retreat	4.8	3.0	1.4	1.7	0.7	2.1
Withdraw	4.3	2.0	3.8	2.2	1.1	0.6
Flee	0.3	0.0	0.4	0.0	0.3	0.2
Freezing	0.2	0.2	0.1	0.0	0.2	0.0
Keep off lying	15.3	3.6	2.7	1.7	1.3	0.6
Squirm	1.8	0.2	0.0	0.1	0.4	0.0
Fall sidew.or backw.	9.9	2.8	1.2	1.2	0.2	0.3
Full subm.post.	4.2	1.6	0.8	0.5	0.4	0.0
Kick	2.1	1.8	0.2	0.3	0.0	0.4
Sidew.defens.post.	17.0	6.1	4.4	5.3	2.6	3.0
Sitting defens.post.	0.1	1.9	0.8	0.2	1.0	0.6
Shrink back	0.4	0.2	0.4	0.2	0.4	0.2
Box	0.2	0.0	0.0	0.0	0.0	0.0
Upright	5.4	2.7	2.1	0.4	0.4	0.2
Standing attention	0.0	0.2	1.8	0.0	1.0	0.4
Parry	8.5	6.6	11.5	4.6	8.0	2.3
Exploration	50.1	42.5	42.2	74.6	45.2	63.4
Stretched attention	0.6	1.6	1.4	2.9	1.7	3.4
Rocking	0.0	0.0	0.0	0.0	0.0	0.2
Sit	40.7	25.3	36.8	30.8	39.6	27.3
Rest	0.0	0.0	0.1	0.0	0.0	0.0
Locomotion	14.5	9.4	11.0	17.0	11.1	14.1
Dally	0.3	0.0	0.0	0.0	0.0	0.0
Jump	0.0	0.0	0.0	0.0	0.0	0.0
Dig	0.2	0.1	0.2	0.8	0.2	1.9
Throw up	0.0	0.0	0.0	0.0	0.0	0.0
Eat	0.0	0.2	0.2	1.0	0.2	0.2
Drink	0.0	0.1	0.0	0.0	0.0	0.0
Groom	2.1	5.6	5.1	9.4	4.6	6.5
Lick wounds	0.0	0.0	4.5	7.3	6.3	4.8
Tail rattle	0.0	0.2	0.0	0.1	0.4	0.0

Table 3. Mean frequency of initiating a behavioural element per observation session by the I-I animals.

	Age (months)							Age (months					
	1	2	3	4	5	6		1	2	3	4	5	6
Approach	19.2	13.2	4.7	9.9	3.3	9.5	Evade	60.1	39.9	29.4	18.8	16.1	15.2
Attend	105.2	78.1	57.2	38.1	33.4	38.9	Retreat	28.9	8.1	1.2	1.1	1.5	3.0
Follow	20.6	18.6	3.7	2.1	1.0	3.0	Withdraw	1.9	3.3	2.4	1.8	3.3	1.3
Investigate	36.5	60.4	35.5	50.6	34.1	41.5	Flee	0.0	0.0	0.0	0.1	0.2	0.0
Nosing	0.1	0.9	0.2	0.0	0.2	2.1	Freezing	0.0	0.0	0.0	0.0	0.0	0.0
Oral inspection	0.1	0.1	0.3	0.3	0.3	0.6	Keep off lying	18.0	6.3	1.3	1.2	1.1	0.8
Anogenital insp.	3.6	7.7	3.2	3.2	2.2	1.1	Squirm	2.9	0.2	0.2	0.0	0.1	0.0
Crawl under	0.8	0.4	0.1	0.0	0.5	0.0	Fall sidew.or backw.	11.9	6.5	1.9	0.2	0.7	0.9
Social grooming	0.1	0.3	0.7	0.1	0.0	0.2	Full subm.post.	0.5	2.0	0.4	0.0	0.0	0.1
Aggressive grooming	4.0	2.8	0.2	0.0	0.0	0.3	Kick	3.4	1.9	2.1	0.7	0.1	4.0
Crawl across	3.3	1.4	0.4	0.4	0.7	0.2	Sidew.defens.post.	37.7	23.1	15.2	3.6	3.4	5.0
Touch	32.6	23.1	8.4	11.4	7.8	8.3	Sitting defens.post.	0.0	0.2	0.8	0.5	0.0	0.4
Take hold	21.2	24.8	5.9	3.8	4.3	0.7	Shrink back	2.8	1.7	1.9	0.6	1.7	0.1
Hold fast	10.9	8.5	1.8	1.7	2.0	0.8	Box	0.0	0.0	1.0	0.7	0.4	0.0
Dash	0.0	0.0	0.0	0.0	0.0	0.2	Upright	4.6	7.1	9.6	3.8	3.1	0.3
Mount	0.2	0.5	0.8	1.5	0.5	0.0	Standing attention	0.0	0.0	1.4	1.4	1.5	1.4
Present passively	0.0	0.1	0.0	0.0	0.0	0.0	Parry	3.3	4.5	9.3	10.5	9.4	4.4
Push	0.0	0.0	0.0	0.0	0.0	0.0	Exploration	59.9	72.4	44.5	75.8	48.4	64.7
Push aside	2.1	0.3	0.2	0.0	0.3	0.1	Stretched attention	0.6	0.8	0.7	2.8	1.7	4.2
Strike	28.6	17.3	3.8	0.9	0.8	1.8	Rocking	0.0	0.1	0.0	0.0	0.0	0.2
Pull	3.1	1.6	0.1	0.0	0.0	0.0	Sit	32.1	28.7	38.2	45.6	41.8	23.7
Snap	0.0	1.2	0.0	0.0	0.0	0.0	Rest	0.0	0.2	0.5	0.0	0.0	0.5
Bend over	0.0	0.0	0.0	0.0	0.0	0.0	Locomotion	22.3	21.8	14.5	17.8	12.0	15.5
Threat	2.3	4.3	9.6	1.8	4.7	1.7	Dally	3.4	1.5	0.0	0.0	0.0	0.0
Impress	0.0	0.0	0.0	0.0	0.0	0.0	Jump	0.4	0.4	0.0	0.0	0.2	0.0
Sideways attack	5.3	8.2	10.3	2.9	4.6	1.5	Dig	1.3	0.8	0.6	1.5	0.4	1.3
Lunge	0.3	0.0	0.1	0.4	0.1	0.0	Throw up	0.0	0.0	0.0	0.0	0.0	0.0
Fight	0.2	0.9	2.3	1.8	1.7	0.6	Eat	0.0	0.0	0.0	0.0	0.1	0.3
Bite	0.6	0.8	2.1	0.2	0.4	0.4	Drink	0.0	0.0	0.0	0.0	0.0	0.0
Push over and backw.	19.1	10.4	2.7	1.1	0.6	0.5	Groom	3.7	5.8	4.3	6.7	4.6	7.3
Keep down	10.6	6.5	2.1	0.9	0.2	0.4	Lick wounds	0.0	0.0	1.4	1.5	6.2	5.5
Chase	0.0	0.0	0.5	0.1	0.0	0.0	Tail rattle	0.0	0.0	0.0	0.0	0.0	0.0

Table 4. Mean frequency of initiating a behavioural element per observation session by the I-G animals

	Age (months)					
	1	2	3	4	5	6
Approach	19.4	13.3	4.8	10.2	3.4	9.8
Attend	105.3	78.9	57.9	38.1	33.5	40.2
Follow	27.1	21.7	4.1	2.1	1.0	3.3
Investigate	55.3	103.0	95.7	113.4	90.4	105.8
Nosing	0.2	1.4	0.3	0.0	0.2	2.5
Oral Inspection	0.1	0.1	0.4	0.6	0.6	1.2
Anogenital inspection	6.9	19.3	7.1	6.2	6.6	3.5
Crawl under	0.8	0.4	0.1	0.0	0.6	0.0
Social grooming	0.1	0.7	1.9	0.2	0.0	0.5
Aggressive grooming	14.4	6.5	0.5	0.0	0.0	0.6
Crawl across	3.3	1.4	0.4	0.4	0.7	0.2
Touch	33.3	23.4	8.4	11.6	7.9	9.3
Take hold	21.2	26.8	6.2	3.8	4.3	1.1
Hold fast	18.2	15.6	6.2	4.9	4.6	1.0
Dash	0.0	0.0	0.0	0.0	0.0	0.2
Mount	0.2	0.6	0.8	1.6	0.6	0.0
Present passively	0.0	0.2	0.0	0.0	0.0	0.0
Push	0.0	0.0	0.0	0.0	0.0	0.0
Push aside	2.1	0.3	0.2	0.0	0.3	0.1
Strike	47.3	28.0	5.2	1.1	0.9	2.8
Pull	4.2	2.5	0.1	0.0	0.0	0.0
Snap	0.0	1.2	0.0	0.0	0.0	0.0
Bend over	0.0	0.0	0.0	0.0	0.0	0.0
Threat	4.2	7.6	28.3	3.1	9.1	3.9
Impress	0.0	0.0	0.0	0.0	0.0	0.0
Sideways attack	6.9	18.0	23.4	4.6	8.8	5.2
Lunge	0.3	0.0	0.2	0.4	0.1	0.0
Fight	0.6	3.0	7.9	5.8	6.7	2.4
Bite	1.0	1.0	2.4	0.2	0.4	0.4
Push over and backw.	19.1	10.5	2.7	1.1	0.6	0.5
Keep down	31.4	23.7	14.9	3.5	0.2	0.7
Chase	0.0	0.0	0.5	0.1	0.0	0.0

	Age (months)					
	1	2	3	4	5	6
Evade	60.6	40.0	29.6	19.3	16.5	16.8
Retreat	31.7	8.1	1.2	1.1	1.5	3.3
Withdraw	1.9	3.3	2.4	1.8	3.3	1.9
Flee	0.0	0.0	0.0	0.1	0.3	0.0
Freezing	0.0	0.0	0.0	0.0	0.0	0.0
Keep off lying	26.5	12.7	2.9	1.4	1.8	1.9
Squirm	5.1	0.3	0.3	0.0	0.1	0.0
Fall sideways or backw.	12.6	6.5	1.9	0.2	0.7	0.9
Full subm. posture	0.8	7.4	1.7	0.0	0.0	0.2
Kick	5.1	3.3	3.6	0.9	0.1	7.9
Sidew.defens. post.	55.6	36.0	25.3	5.6	4.7	11.2
Sitting defens. post.	0.0	0.6	1.2	1.6	0.0	0.6
Shrink back	2.8	1.7	2.0	0.6	1.7	0.1
Box	0.0	0.0	1.8	2.0	0.7	0.0
Upright	7.4	15.8	35.2	9.1	19.5	1.1
Standing attention	0.0	0.0	7.4	4.0	10.8	4.1
Parry	5.0	9.7	30.5	30.8	27.9	17.4
Exploration	137.8	202.8	222.8	343.2	265.3	333.0
Stretched attention	2.0	7.5	3.2	8.7	3.5	10.8
Rocking	0.0	0.6	0.0	0.0	0.0	0.3
Sit	76.7	87.3	147.3	148.4	208.4	131.9
Rest	0.0	0.2	4.3	0.0	0.0	1.4
Locomotion	27.9	25.0	18.3	19.5	14.0	20.0
Dally	5.5	1.5	0.0	0.0	0.0	0.0
Jump	0.6	0.4	0.0	0.0	0.3	0.0
Dig	2.4	0.9	1.4	2.8	0.5	2.5
Throw up	0.0	0.0	0.0	0.0	0.0	0.0
Eat	0.0	0.0	0.0	0.0	0.4	1.9
Drink	0.0	0.0	0.0	0.0	0.0	0.0
Groom	9.1	19.3	40.8	65.6	56.5	39.8
Lick wounds	0.0	0.0	34.3	20.3	79.9	85.8
Tail rattle	0.0	0.0	0.0	0.0	0.0	0.0

Table 5. Mean total time (seconds) spent on different activities per observation session by the I-G animals.

	Age (months)							Age (months)					
	1	2	3	4	5	6		1	2	3	4	5	6
Approach	22.2	15.3	8.7	8.1	7.2	9.8	Evade	38.7	24.3	13.4	12.4	11.0	6.4
Attend	83.3	49.2	55.6	33.8	35.1	32.3	Retreat	19.5	10.6	2.3	0.3	1.2	0.6
Follow	24.2	11.2	2.7	1.1	1.7	4.0	Withdraw	3.8	4.3	5.2	1.4	2.6	1.6
Investigate	34.3	38.4	33.1	35.0	29.1	36.6	Flee	0.0	0.1	0.6	0.2	0.0	0.2
Nosing	0.1	0.9	0.2	0.0	0.2	2.2	Freezing	0.0	0.0	0.2	0.1	0.0	0.1
Oral inspection	0.3	0.3	0.5	0.5	0.5	1.3	Keep off lying	36.1	13.7	6.4	3.0	2.6	0.8
Anogenital insp.	2.2	2.6	10.4	9.4	7.0	10.3	Squirm	6.1	0.3	0.1	0.0	0.1	0.0
Crawl under	0.2	0.1	0.2	2.7	0.9	2.5	Fall sidew.or backw.	17.7	8.7	3.1	1.3	1.0	0.5
Social grooming	0.0	0.8	0.0	0.0	0.0	0.6	Full subm.post.	2.1	3.4	1.7	0.5	0.2	0.2
Aggressive grooming	0.9	0.5	0.0	0.1	0.0	0.1	Kick	6.6	3.4	0.2	0.0	0.0	0.0
Crawl across	3.4	0.8	0.0	0.4	0.5	0.1	Sidew.defens.post.	29.5	19.4	4.5	3.7	2.3	1.3
Touch	44.9	22.2	18.8	9.0	8.5	7.8	Sitting defens.post.	0.6	5.9	3.6	0.8	1.1	0.6
Take hold	29.5	16.7	9.9	2.7	3.5	3.4	Shrink back	1.1	2.6	0.4	0.9	0.3	0.0
Hold fast	12.9	10.0	4.2	0.9	1.6	1.7	Box	0.1	0.0	1.0	0.7	0.4	0.0
Dash	0.0	0.0	0.0	0.0	0.0	0.0	Upright	5.4	8.0	10.3	3.6	3.0	0.6
Mount	1.8	0.1	0.0	0.5	0.1	0.2	Standing attention	0.0	0.0	1.4	1.1	1.4	1.4
Present passively	0.0	0.0	0.0	0.0	0.0	0.0	Parry	6.6	11.8	22.3	11.7	12.0	3.4
Push	0.0	0.0	0.0	0.0	0.0	0.1	Exploration	71.7	72.2	51.3	77.6	59.8	67.2
Push aside	2.3	0.1	0.1	0.0	0.0	0.1	Stretched attention	0.4	0.4	1.5	3.8	2.5	5.2
Strike	21.3	12.4	2.5	0.4	0.6	0.8	Rocking	0.0	0.0	0.0	0.0	0.0	0.3
Pull	6.0	2.7	0.3	0.3	0.0	2.4	Sit	35.5	27.7	28.0	42.6	28.4	18.7
Snap	0.0	0.7	0.1	0.0	0.1	0.0	Rest	0.0	0.2	0.0	0.0	0.0	0.0
Bend over	0.0	0.0	0.0	0.0	0.0	0.0	Locomotion	13.9	20.4	13.2	18.3	14.6	15.5
Threat	0.1	0.0	0.1	0.6	0.2	0.0	Dally	1.3	0.3	0.0	0.0	0.0	0.0
Impress	0.1	0.0	0.0	0.0	0.0	0.0	Jump	1.5	0.1	0.0	0.0	0.0	0.0
Sideways attack	0.4	0.1	0.0	0.4	0.1	0.0	Dig	5.0	4.4	0.8	1.5	0.5	1.7
Lunge	0.0	0.4	0.0	0.0	0.1	0.0	Throw up	0.0	0.1	0.0	0.1	0.1	0.2
Fight	0.2	0.9	2.3	1.8	1.7	0.6	Eat	0.0	0.1	0.0	0.9	0.0	2.2
Bite	0.1	0.3	0.0	0.1	0.0	0.0	Drink	0.0	1.1	0.0	0.0	0.1	0.0
Push over and backw.	9.7	6.8	1.4	0.2	0.4	0.6	Groom	1.2	4.7	4.0	7.5	6.7	6.9
Keep down	4.0	3.6	0.4	0.0	0.4	0.7	Lick wounds	0.0	0.0	0.1	0.0	2.8	0.3
Chase	0.0	0.0	0.0	0.0	0.2	0.0	Tail rattle	0.0	0.0	0.0	0.0	0.1	0.0

Table 6. Mean frequency of initiating a behavioural element per observation session by the G-I animals

	Age (months)					
	1	2	3	4	5	6
Approach	22.4	15.4	9.0	8.3	7.5	11.5
Attend	83.5	49.3	56.4	33.9	35.1	32.9
Follow	28.5	11.9	2.9	1.2	1.8	4.6
Investigate	47.5	57.1	69.9	60.8	55.6	68.8
Nosing	0.2	1.4	0.3	0.0	0.2	2.8
Oral inspection	0.3	0.3	0.8	0.8	1.0	2.8
Anogenital insp.	3.2	5.0	24.8	18.9	19.5	31.0
Crawl under	0.2	0.1	0.2	2.7	0.9	2.6
Social grooming	0.0	3.0	0.0	0.0	0.0	3.8
Aggressive grooming	2.1	0.9	0.0	0.1	0.0	0.4
Crawl across	3.4	0.8	0.0	0.4	0.5	0.1
Touch	45.4	22.2	19.6	9.2	8.5	8.0
Take hold	29.9	17.3	10.6	2.7	3.5	5.8
Hold fast	20.6	21.4	8.9	1.6	2.6	4.0
Dash	0.0	0.0	0.0	0.0	0.0	0.0
Mount	2.0	0.1	0.0	0.5	0.1	0.4
Present passively	0.0	0.0	0.0	0.0	0.0	0.0
Push	0.0	0.0	0.0	0.0	0.0	0.2
Push aside	2.4	0.1	0.1	0.0	0.0	0.2
Strike	35.6	22.6	4.1	0.4	0.7	1.6
Pull	8.8	4.6	0.6	0.3	0.0	5.2
Snap	0.0	0.8	0.1	0.0	0.2	0.0
Bend over	0.0	0.0	0.0	0.0	0.0	0.0
Threat	0.1	0.0	0.1	1.0	0.6	0.0
Impress	0.1	0.0	0.0	0.0	0.0	0.0
Sideways attack	0.4	0.1	0.0	0.5	0.1	0.0
Lunge	0.0	0.5	0.0	0.0	0.2	0.0
Fight	0.6	3.0	7.9	5.8	6.7	2.4
Bite	0.2	0.4	0.0	0.1	0.0	0.0
Push over and backw.	10.1	7.3	1.4	0.2	0.4	0.6
Keep down	12.4	12.1	1.3	0.0	0.9	2.3
Chase	0.0	0.0	0.0	0.0	0.4	0.0

	Age (months)					
	1	2	3	4	5	6
Evade	39.1	24.4	13.4	12.4	11.8	7.1
Retreat	21.1	11.4	2.3	0.3	1.2	0.7
Withdraw	3.9	4.3	5.2	1.4	2.6	1.6
Flee	0.0	0.1	0.6	0.3	0.0	0.3
Freezing	0.0	0.0	24.6	14.4	0.0	0.1
Keep off lying	67.1	31.5	14.7	6.7	4.4	1.5
Squirm	15.5	1.2	0.1	0.0	0.1	0.0
Fall sidew.or backw.	17.7	8.7	3.1	1.3	1.0	0.5
Full subm.post.	5.4	11.9	14.2	2.1	3.5	3.2
Kick	7.8	4.8	0.2	0.0	0.0	0.0
Sidew.defens.post.	38.3	25.6	6.7	5.4	3.7	1.6
Sitting defens.post.	1.1	14.7	17.0	2.2	2.6	1.7
Shrink back	1.1	2.6	0.5	0.9	0.3	0.0
Box	0.1	0.0	1.8	2.0	0.7	0.0
Upright	9.1	16.6	36.8	11.1	19.8	1.5
Standing attention	0.0	0.0	4.2	3.4	10.6	6.1
Parry	13.1	42.0	83.3	34.1	38.6	12.0
Exploration	192.3	253.3	222.0	395.7	368.8	416.2
Stretched attention	1.1	1.9	14.0	8.4	8.3	12.5
Rocking	0.0	0.0	0.0	0.0	0.0	0.3
Sit	71.9	103.3	144.3	130.7	120.2	117.0
Rest	0.0	0.3	0.0	0.0	0.0	0.0
Locomotion	16.8	24.8	15.2	20.0	16.0	20.8
Dally	2.0	0.4	0.0	0.0	0.0	0.0
Jump	1.6	0.1	0.0	0.0	0.0	0.0
Dig	9.4	10.8	2.5	3.3	1.4	2.4
Throw up	0.0	0.1	0.0	0.1	0.2	0.3
Eat	0.0	0.3	0.0	12.4	0.0	16.3
Drink	0.0	22.3	0.0	0.0	2.8	0.0
Groom	4.5	24.9	52.9	82.0	103.5	78.0
Lick wounds	0.0	0.0	1.4	0.0	29.8	6.2
Tail rattle	0.0	0.0	0.0	0.0	0.1	0.0

Table 7. Mean total time (seconds) spent on different activities per observation session by the G-I animals

	Age (months)							Age (months)					
	1	2	3	4	5	6		1	2	3	4	5	6
Approach	19.8	18.7	13.6	11.4	11.0	7.7	Evade	25.5	23.2	12.9	9.9	13.9	7.2
Attend	29.5	26.3	30.4	28.3	33.5	33.4	Retreat	6.2	5.8	2.4	0.6	0.9	0.5
Follow	10.9	8.3	5.1	3.0	5.0	3.5	Withdraw	0.5	3.1	1.5	1.5	1.3	1.5
Investigate	24.8	35.7	38.6	32.5	38.7	45.2	Flee	0.0	0.0	0.0	0.1	0.0	0.0
Nosing	0.5	2.1	2.5	1.8	2.4	0.5	Freezing	0.0	0.2	0.0	0.0	0.0	0.0
Oral inspection	1.4	1.4	1.3	2.1	1.8	3.5	Keep off lying	11.6	12.8	4.8	4.0	3.2	0.7
Anogenital insp.	4.5	6.0	12.1	17.2	22.1	17.8	Squirm	0.4	1.2	0.0	0.1	0.1	0.0
Crawl under	0.5	1.2	0.5	1.9	0.8	0.6	Fall sidew.or backw.	1.8	3.4	0.0	0.3	1.0	0.0
Social grooming	0.0	0.6	0.4	0.0	0.1	0.1	Full subm.post.	0.0	0.6	0.0	0.0	0.5	0.0
Aggressive grooming	0.1	0.0	0.0	0.0	0.0	0.0	Kick	1.2	0.9	0.3	0.5	0.5	0.2
Crawl across	3.1	2.5	0.4	0.6	0.6	0.6	Sidew.defens.post.	12.6	13.0	2.7	2.4	3.2	0.4
Touch	19.8	12.0	7.3	7.3	9.5	11.1	Sitting defens.post.	0.1	0.1	0.0	0.5	0.7	0.0
Take hold	13.7	11.7	2.9	3.9	5.0	1.8	Shrink back	0.6	0.0	0.1	0.0	0.4	0.3
Hold fast	2.9	1.4	0.2	0.4	0.6	0.5	Box	0.0	0.0	0.2	0.2	0.0	0.0
Dash	0.0	0.0	0.0	0.0	0.0	0.0	Upright	1.2	3.2	0.4	2.6	1.6	0.2
Mount	5.5	1.6	1.8	1.1	0.7	0.9	Standing attention	0.0	0.0	0.0	0.2	0.9	0.2
Present passively	0.0	0.0	0.0	0.0	0.0	0.0	Parry	0.1	0.2	2.0	1.2	4.2	1.9
Push	0.0	0.0	0.0	0.0	0.0	0.0	Exploration	95.6	89.0	82.2	80.9	89.6	91.7
Push aside	0.0	0.4	0.4	0.3	0.4	0.5	Stretched attention	0.1	1.0	2.3	0.6	1.2	2.4
Strike	9.1	8.9	2.6	0.7	1.7	0.4	Rocking	0.0	0.1	0.0	0.0	0.0	0.0
Pull	0.4	0.7	0.7	0.1	0.0	0.6	Sit	21.8	21.3	14.7	14.9	13.1	17.6
Snap	0.0	0.0	0.0	0.0	0.0	0.0	Rest	0.0	0.0	0.0	0.0	0.0	0.1
Bend over	0.0	0.0	0.0	0.0	0.0	0.0	Locomotion	27.2	27.2	22.0	20.2	23.7	20.1
Threat	0.1	0.0	0.1	1.1	0.3	0.0	Dally	1.1	0.1	0.0	0.0	0.0	0.0
Impress	0.0	0.0	0.0	0.0	0.0	0.0	Jump	1.0	0.3	0.1	0.0	0.0	0.0
Sideways attack	0.0	0.0	0.0	0.5	0.8	0.2	Dig	5.3	6.6	3.7	3.3	3.1	2.5
Lunge	0.0	0.0	0.0	0.1	0.0	0.0	Throw up	0.0	0.2	0.2	0.0	0.0	0.0
Fight	0.0	0.6	0.0	1.0	0.2	0.2	Eat	1.4	0.2	0.7	0.3	0.0	0.7
Bite	0.0	0.5	0.0	0.1	0.2	0.0	Drink	0.3	0.5	0.6	0.5	0.1	0.1
Push over and backw.	1.3	3.2	0.0	0.3	0.8	0.1	Groom	3.8	4.8	6.5	6.0	4.4	6.7
Keep down	0.9	3.8	0.0	0.2	0.7	0.0	Lick wounds	0.0	0.0	0.0	0.0	0.0	0.0
Chase	0.0	0.0	0.0	0.1	0.0	0.0	Tail rattle	0.0	0.0	0.0	0.0	0.0	0.0

Table 8. Mean frequency of initiating a behavioural element per observation session by the G-GU animals

	Age (months)					
	1	2	3	4	5	6
Approach	19.9	18.9	14.2	11.7	11.1	7.9
Attend	29.5	26.3	30.4	28.3	33.7	33.4
Follow	12.3	9.0	6.0	3.2	5.8	4.2
Investigate	29.7	44.9	51.1	40.5	52.3	62.6
Nosing	0.5	2.3	2.6	1.8	2.4	0.6
Oral inspection	1.9	1.6	1.7	2.5	2.5	5.6
Anogenital insp.	8.9	13.9	21.1	33.6	40.5	31.7
Crawl under	0.5	1.2	0.5	1.9	0.8	0.6
Social grooming	0.0	2.1	0.9	0.0	0.4	0.2
Aggressive grooming	0.1	0.0	0.0	0.0	0.0	0.0
Crawl across	3.1	2.5	0.4	0.6	0.6	0.6
Touch	20.4	12.0	7.3	7.5	9.5	11.1
Take hold	13.7	11.7	2.9	3.9	5.0	1.8
Hold fast	3.5	1.9	0.2	1.1	1.1	0.7
Dash	0.0	0.0	0.0	0.0	0.0	0.0
Mount	5.5	1.6	1.8	1.1	0.7	0.9
Present passively	0.0	0.0	0.0	0.0	0.0	0.0
Push	0.0	0.0	0.0	0.0	0.0	0.0
Push aside	0.0	0.6	0.4	0.3	0.4	0.5
Strike	14.6	19.4	6.3	0.8	2.2	0.4
Pull	0.4	1.0	0.7	0.2	0.0	0.8
Snap	0.0	0.0	0.0	0.0	0.0	0.0
Bend over	0.0	0.0	0.0	0.0	0.0	0.0
Threat	0.3	0.0	0.1	3.2	1.2	0.0
Impress	0.0	0.0	0.0	0.0	0.0	0.0
Sideways attack	0.0	0.0	0.0	0.6	1.6	0.3
Lunge	0.0	0.0	0.0	0.1	0.0	0.0
Fight	0.0	1.8	0.0	2.0	0.4	0.2
Bite	0.0	0.7	0.0	0.1	0.4	0.0
Push over and backw.	1.3	3.2	0.0	0.3	0.8	0.1
Keep down	1.4	19.9	0.0	0.5	5.3	0.0
Chase	0.0	0.0	0.0	0.1	0.0	0.0

	Age (months)					
	1	2	3	4	5	6
Evade	25.7	23.2	12.9	9.9	13.9	7.9
Retreat	6.4	6.2	2.4	0.6	0.9	2.9
Withdraw	0.5	3.1	1.5	1.5	1.3	1.5
Flee	0.0	0.0	0.0	0.1	0.0	0.0
Freezing	0.0	3.0	0.0	0.0	0.0	0.0
Keep off lying	14.5	31.5	5.7	4.9	7.2	0.8
Squirm	0.4	1.8	0.0	0.1	0.1	0.0
Fall sidew.or backw.	1.8	3.4	0.0	0.3	1.0	0.0
Full subm.post.	0.0	2.6	0.0	0.0	2.8	0.0
Kick	1.3	1.2	0.4	0.7	0.6	0.2
Sidew.defens.post.	14.2	14.4	2.8	3.0	4.2	0.7
Sitting defens.post.	0.1	0.3	0.0	2.1	1.4	0.0
Shrink back	0.6	0.0	0.1	0.0	0.4	0.3
Box	0.0	0.0	0.8	0.8	0.0	0.0
Upright	1.3	8.8	0.5	11.6	6.2	0.8
Standing attention	0.0	0.0	0.0	3.0	2.7	0.2
Parry	0.1	0.4	2.9	7.6	9.5	4.1
Exploration	518.3	483.2	561.0	531.1	530.5	548.5
Stretched attention	0.2	4.1	8.1	4.2	2.2	8.1
Rocking	0.0	0.1	0.0	0.0	0.0	0.0
Sit	60.9	38.9	51.2	58.7	49.8	40.9
Rest	0.0	0.0	0.0	0.0	0.0	2.4
Locomotion	31.2	33.4	26.0	21.8	25.2	26.9
Dally	1.2	0.1	0.0	0.0	0.0	0.0
Jump	1.2	0.5	0.2	0.0	0.0	0.0
Dig	8.6	12.8	8.5	5.3	5.5	4.1
Throw up	0.0	0.4	0.3	0.0	0.0	0.0
Eat	18.9	0.4	6.2	7.5	0.0	2.7
Drink	5.1	9.1	7.1	7.3	4.3	2.7
Groom	19.9	20.5	52.7	71.7	51.6	80.6
Lick wounds	0.0	0.0	0.0	0.0	0.0	0.0
Tail rattle	0.0	0.0	0.0	0.0	0.0	0.1

Table 9. Mean total time (seconds) spent on different activities per observation session by the G-GU animals

	Age (months)					
	1	2	3	4	5	6
Approach	23.3	19.6	14.2	11.3	10.5	8.3
Attend	34.3	31.6	33.0	25.1	24.6	22.5
Follow	17.3	10.1	4.2	2.2	1.6	3.3
Investigate	23.7	32.7	32.4	32.1	35.8	36.8
Nosing	1.0	1.6	1.7	1.0	0.9	1.2
Oral inspection	1.1	0.1	1.3	0.5	0.9	0.6
Anogenital insp.	2.4	5.2	8.2	10.7	9.1	12.1
Crawl under	0.8	0.6	0.9	1.3	0.4	0.7
Social grooming	0.0	0.3	0.1	0.7	0.9	0.0
Aggressive grooming	0.1	0.3	0.0	0.0	0.0	0.0
Crawl across	3.4	2.2	0.4	0.6	0.5	0.4
Touch	23.9	11.0	7.7	5.9	8.9	9.0
Take hold	16.8	10.8	5.1	3.9	2.7	0.6
Hold fast	5.1	1.6	1.1	1.9	0.5	0.2
Dash	0.0	0.0	0.0	0.0	0.0	0.0
Mount	2.8	4.4	1.7	1.0	0.5	0.1
Present passively	0.0	0.0	0.0	0.0	0.0	0.0
Push	0.0	0.0	0.0	0.0	0.0	0.0
Push aside	0.3	0.7	0.2	1.0	0.1	0.3
Strike	15.1	9.0	3.0	3.8	0.8	0.8
Pull	1.3	1.7	0.6	0.3	1.5	0.0
Snap	0.0	0.0	0.0	0.0	0.0	0.0
Bend over	0.0	0.0	0.0	0.0	0.0	0.0
Threat	0.0	0.0	0.0	0.1	0.0	0.0
Impress	0.0	0.0	0.0	0.0	0.0	0.0
Sideways attack	0.0	0.0	0.3	0.6	0.0	0.0
Lunge	0.0	0.0	0.0	0.0	0.0	0.0
Fight	0.0	0.0	0.0	0.4	0.0	0.0
Bite	0.0	0.1	0.1	0.1	0.0	0.0
Push over and backw.	1.9	4.5	0.6	2.1	0.0	0.0
Keep down	1.2	3.4	1.3	1.2	0.0	0.0
Chase	0.0	0.0	0.0	0.0	0.0	0.0

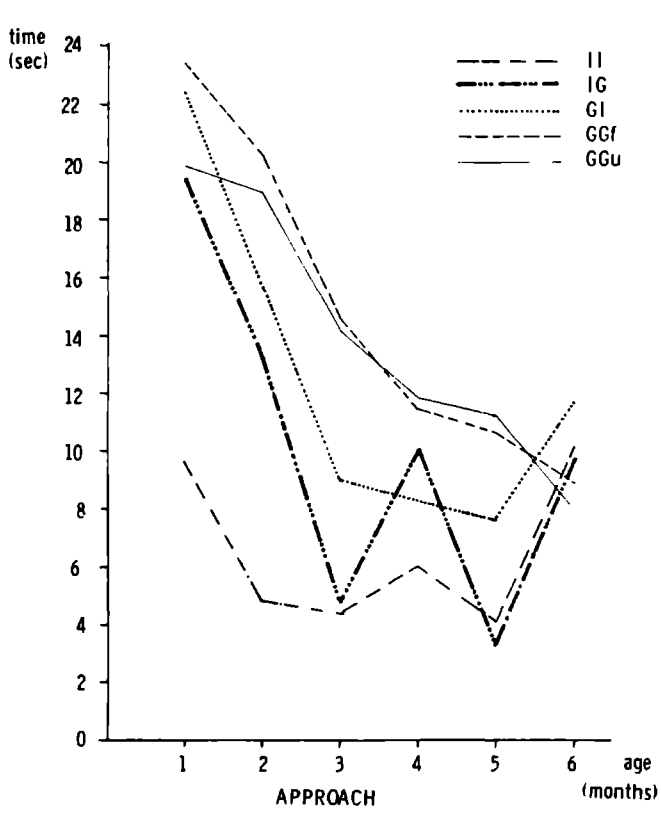
	Age (months)					
	1	2	3	4	5	6
Evade	32.0	24.9	14.1	9.7	7.4	6.3
Retreat	12.2	7.1	2.4	0.9	0.3	0.3
Withdraw	1.3	1.5	1.5	2.5	0.5	0.4
Flee	0.0	0.0	0.0	0.0	0.0	0.0
Freezing	0.0	0.2	0.0	0.0	0.0	0.0
Keep off lying	19.5	10.6	5.4	6.0	1.0	1.0
Squirm	0.2	1.3	0.9	0.6	0.0	0.0
Fall sidew.or backw.	2.2	3.9	1.1	1.8	0.0	0.0
Full subm.post.	0.0	0.3	0.7	0.2	0.0	0.0
Kick	1.9	0.3	0.7	0.6	0.2	0.3
Sidew.defens.post.	15.6	10.8	4.7	3.6	0.9	0.1
Sitting defens.post.	0.0	0.0	0.3	0.5	0.0	0.0
Shrink back	0.2	0.2	0.1	0.1	0.0	0.0
Box	0.0	0.0	0.0	0.0	0.0	0.0
Upright	1.4	5.2	2.0	1.9	0.0	0.0
Standing attention	0.0	0.0	0.0	2.1	0.0	0.0
Parry	0.1	0.2	0.5	2.3	0.7	1.1
Exploration	100.9	84.5	82.5	72.5	81.7	88.0
Stretched attention	0.0	1.4	1.3	1.1	2.4	1.5
Rocking	0.0	0.0	0.2	0.0	0.0	0.0
Sit	20.1	20.4	16.0	14.9	14.8	11.8
Rest	0.0	0.0	0.0	0.0	0.0	0.0
Locomotion	29.5	25.3	30.2	21.1	20.9	23.7
Dally	1.7	0.2	0.0	0.0	0.0	0.0
Jump	0.5	0.0	0.0	0.1	0.0	0.0
Dig	6.3	5.5	3.5	4.6	3.6	4.1
Throw up	0.3	0.0	0.0	0.0	0.0	0.0
Eat	1.3	0.3	1.1	0.1	0.3	0.8
Drink	0.2	0.1	0.0	0.0	0.1	0.1
Groom	4.0	5.2	4.4	5.8	6.1	7.8
Lick wounds	0.1	0.0	0.0	0.0	0.0	0.0
Tail rattle	0.0	0.0	0.0	0.0	0.0	0.0

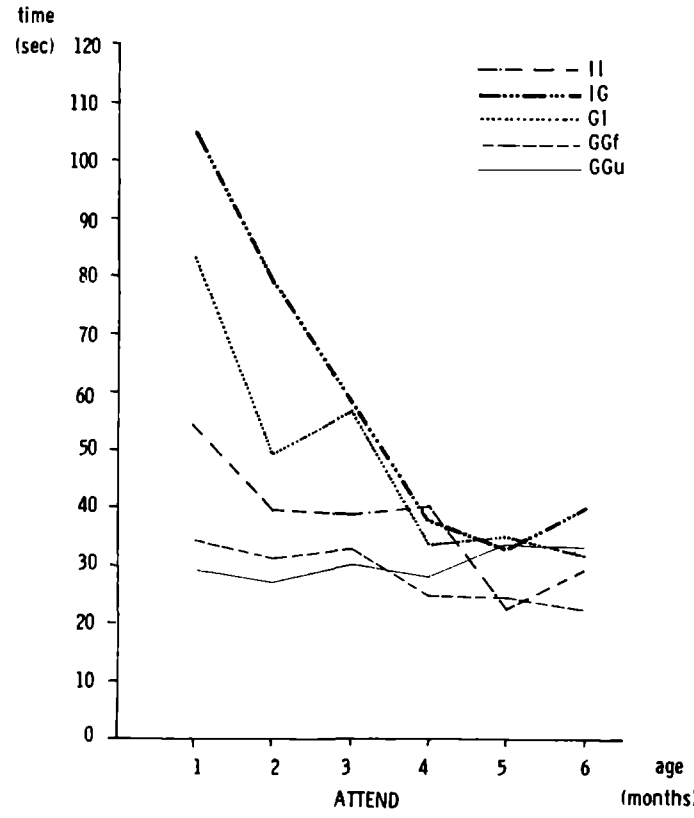
Table 10. Mean frequency of initiating a behavioural element per observation session by the G-GF animals

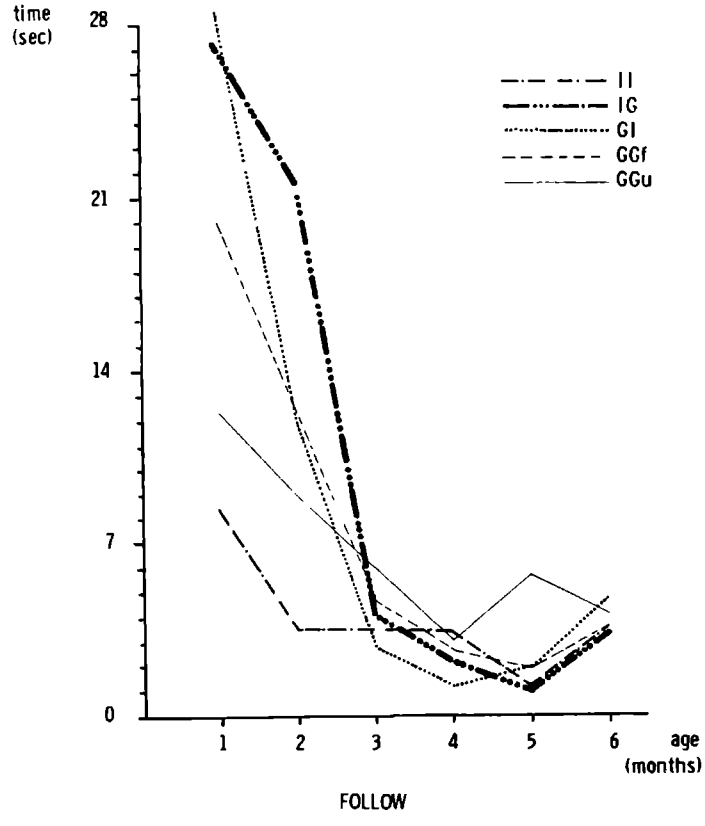
	Age (months)					
	1	2	3	4	5	6
Approach	23.5	20.3	14.5	11.5	10.7	8.8
Attend	34.3	31.6	33.0	25.1	24.6	22.5
Follow	20.0	12.3	4.8	2.7	1.8	3.7
Investigate	27.0	41.7	42.1	42.3	46.9	48.1
Nosing	1.0	1.6	2.3	1.2	0.9	1.2
Oral inspection	1.1	0.1	1.4	0.8	1.2	0.6
Anogenital insp.	3.1	10.5	15.9	20.4	15.5	23.0
Crawl under	0.8	0.6	0.9	1.3	0.4	0.7
Social grooming	0.0	1.4	0.8	2.8	4.5	0.0
Aggressive grooming	0.1	0.6	0.0	0.0	0.0	0.0
Crawl across	3.4	2.2	0.4	0.6	0.5	0.4
Touch	23.9	11.1	7.7	5.9	8.9	9.1
Take hold	16.8	11.1	5.1	3.9	2.7	0.6
Hold fast	7.2	2.2	1.7	3.0	0.5	0.2
Dash	0.0	0.0	0.0	0.0	0.0	0.0
Mount	2.8	4.4	1.8	1.0	0.5	0.1
Present passively	0.0	0.0	0.0	0.0	0.0	0.0
Push	0.0	0.0	0.0	0.0	0.0	0.0
Push aside	0.4	0.7	0.3	1.0	0.1	0.3
Strike	231.1	24.3	7.2	12.6	0.8	1.1
Pull	1.7	2.2	0.6	0.7	2.1	0.0
Snap	0.0	0.0	0.0	0.0	0.0	0.0
Bend over	0.0	0.0	0.0	0.0	0.0	0.0
Threat	0.0	0.0	0.0	0.3	0.0	0.0
Impress	0.0	0.0	0.0	0.0	0.0	0.0
Sideways attack	0.0	0.0	0.4	1.0	0.0	0.0
Lunge	0.0	0.0	0.0	0.0	0.0	0.0
Fight	0.0	0.0	0.0	1.0	0.0	0.0
Bite	0.0	0.1	0.1	0.1	0.0	0.0
Push over and backw.	1.9	4.6	0.6	2.1	0.0	0.0
Keep down	3.0	14.0	11.6	4.3	0.0	0.0
Chase	0.0	0.0	0.0	0.0	0.0	0.0

	Age (months)					
	1	2	3	4	5	6
Evade	32.7	25.7	14.4	9.7	7.5	6.3
Retreat	13.0	7.6	2.4	1.0	0.3	11.3
Withdraw	1.4	1.5	1.5	2.5	0.5	0.4
Flee	0.0	0.0	0.0	0.0	0.0	0.0
Freezing	0.0	0.2	0.0	0.0	0.0	0.0
Keep off lying	27.2	22.1	13.7	9.0	1.0	1.2
Squirm	0.3	2.7	1.1	0.8	0.0	0.0
Fall sidew.or backw.	2.2	3.9	1.1	1.8	0.0	0.0
Full subm.post.	0.0	1.4	4.4	2.2	0.0	0.0
Kick	2.1	0.4	0.9	0.8	0.4	0.5
Sidew.defens.post.	17.3	13.2	5.4	6.5	1.0	0.1
Sitting defens.post.	0.0	0.0	1.3	1.3	0.0	0.0
Shrink back	0.2	0.2	0.1	0.1	0.0	0.0
Box	0.0	0.0	0.0	0.0	0.0	0.0
Upright	1.6	7.7	4.8	4.8	0.0	0.0
Standing attention	0.0	0.0	0.0	11.5	0.0	0.0
Parry	0.1	0.2	0.8	6.3	1.2	1.5
Exploration	481.7	460.0	546.0	509.2	614.5	560.0
Stretched attention	0.0	8.7	9.6	1.4	7.7	3.3
Rocking	0.0	0.0	0.8	0.0	0.0	0.0
Sit	50.7	49.0	53.3	66.2	56.7	37.7
Rest	0.0	0.0	0.0	0.0	0.0	0.0
Locomotion	33.6	29.0	36.5	22.5	23.0	26.9
Dally	2.3	0.2	0.0	0.0	0.0	0.0
Jump	0.5	0.0	0.0	0.1	0.0	0.0
Dig	10.6	10.1	6.4	9.2	5.2	6.3
Throw up	0.6	0.0	0.0	0.0	0.0	0.0
Eat	11.3	1.2	16.7	0.7	0.5	3.9
Drink	4.1	5.8	0.0	0.0	0.5	4.9
Groom	11.3	52.6	25.5	86.6	56.9	115.3
Lick wounds	0.1	0.0	0.0	0.0	0.0	0.0
Tail rattle	0.0	0.0	0.0	0.0	0.0	0.0

Table 11. Mean total time (seconds) spent on different activities per observation session by the G-GF animals







Figs. 1, 2 and 3. Total time spent on the social exploration activities at distance *approach*, *attend* and *follow*.

APPROACH

	Df.	Frequ.	Tot.Time		Df.	Frequ.	Tot.time
Rearing	1	43.91"	43.98"	Rearing cond.	1	21.76"	22.49"
Testpartner	1	15.51"	13.13"	Familiarity	1	0.66	0.81
Age	5	22.16"	20.96"	Age	5	22.25"	21.68"
Rearing X Partner	1	1.93	2.06	Rearing X Age	5	5.69"	5.74"
Rearing X Age	5	3.79"	3.33"	Familiarity X Age	5	0.31	0.33
Partner X Age	5	1.78	2.22	Error	162	31.66	32.37
Rearing X Partner X Age	5	3.44"	3.20"				
Error	216	30.50	32.09				

ATTEND

Rearing	1	18.30"	19.34"	Rearing cond.	1	194.00"	199.55"
Testpartner	1	0.68	0.53	Familiarity	1	0.51	0.52
Age	5	31.40"	30.34"	Age	5	33.68"	33.36"
Rearing X Partner	1	95.30"	93.30"	Rearing X Age	5	12.57"	12.49"
Rearing X Age	5	5.54"	5.34"	Familiarity X Age	5	1.42	1.43
Partner X Age	5	0.94	1.07	Error	162	174.69	175.52
Rearing X Partner X Age	5	15.96"	15.43"				
Error	216	242.90	250.41				

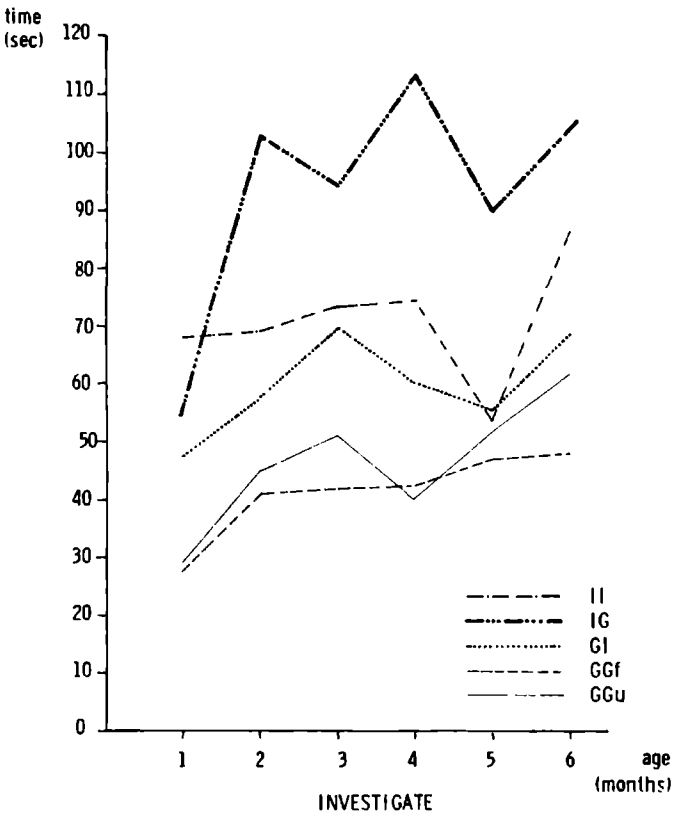
FOLLOW

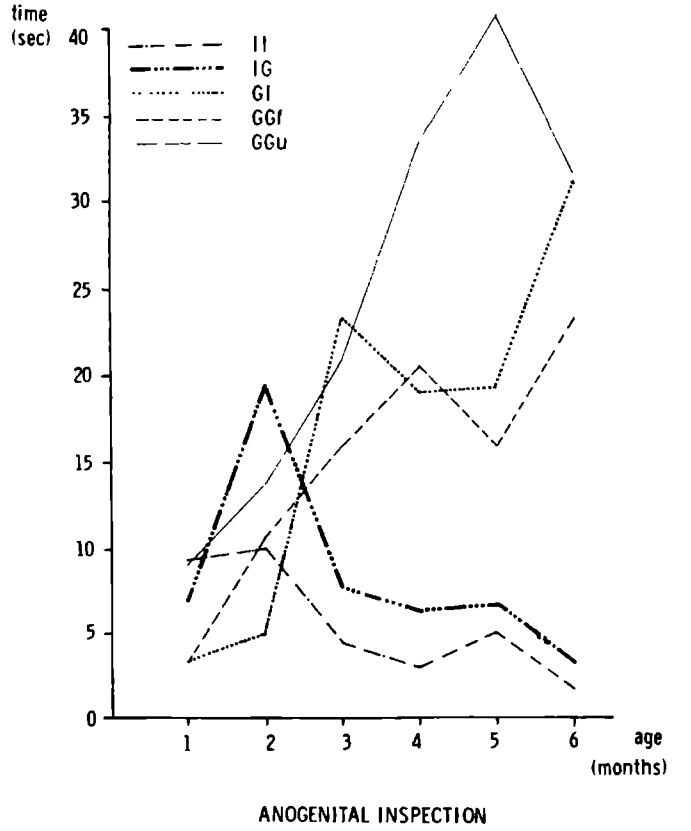
Rearing	1	2.88	0.81	Rearing cond.	1	5.03'	6.31'
Testpartner	1	7.48"	6.85"	Familiarity	1	0.23	0.41
Age	5	45.80"	45.07"	Age	5	38.87"	38.52"
Rearing X Partner	1	25.40"	22.49"	Rearing X Age	5	0.79	0.48
Rearing X Age	5	1.44	0.89	Familiarity X Age	5	1.83	1.78
Partner X Age	5	2.13	2.03	Error	162	30.47	47.34
Rearing X Partner X Age	5	16.87"	16.86"				
Error	216	25.98	39.88				

' $.05 \geq p > .01$

" $.01 \geq p$

Table 12. F-values of frequencies and total time on the activities *approach*, *attend* and *follow*.





Figs. 4 and 5. Total time spent on the social exploration activities in physical contact *investigate* and *anogenital inspection*.

INVESTIGATE

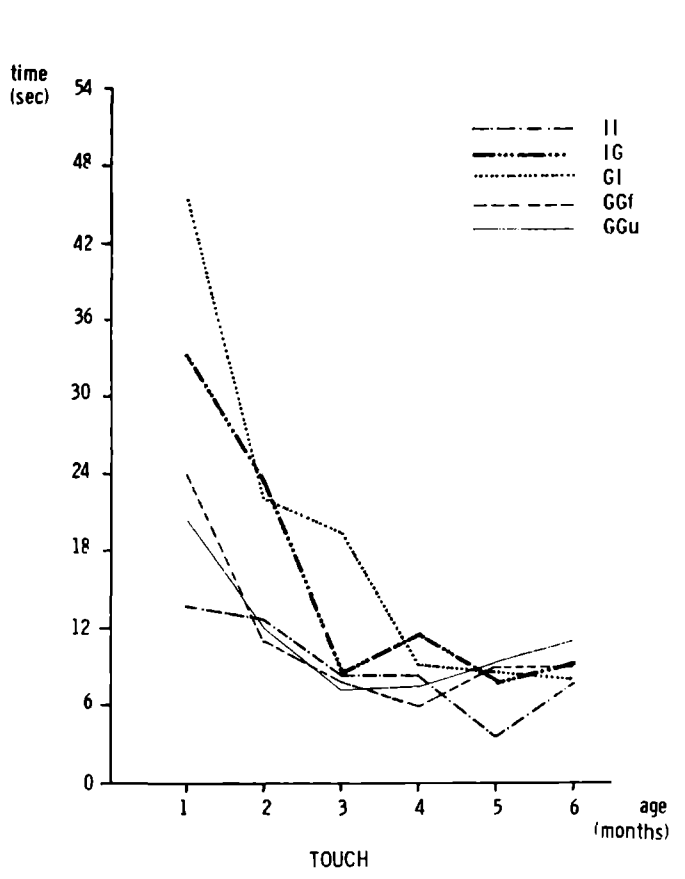
	Df.	Freq.	Tot.time		Df.	Freq.	Tot.Time
Rearing	1	0.45	62.97"	Rearing cond.	1	19.36"	172.57"
Testpartner	1	19.28"	1.74	Familiarity	1	2.40	1.58
Age	5	4.60"	5.41"	Age	5	5.61"	8.95"
Rearing X Partner	1	12.37"	23.87"	Rearing X Age	5	4.63"	1.29
Rearing X Age	5	2.58'	1.04	Familiarity X Age	5	0.28	0.28
Partner X Age	5	2.04	1.49	Error	162	167.99	575.60
Rearing X Partner X Age	5	2.97'	1.05				
Error	216	176.61	809.20				

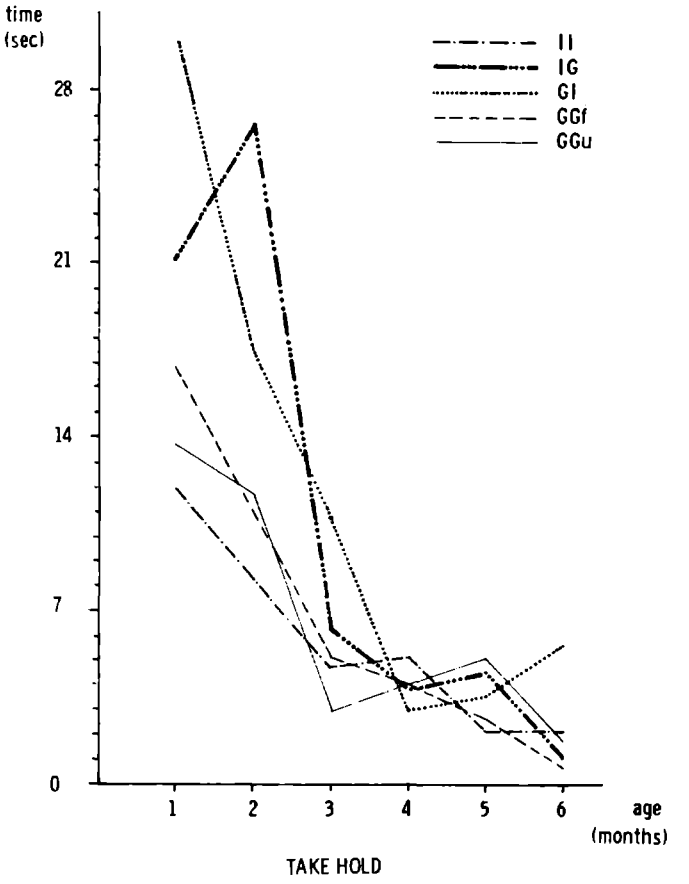
ANOGENITAL INSPECTION

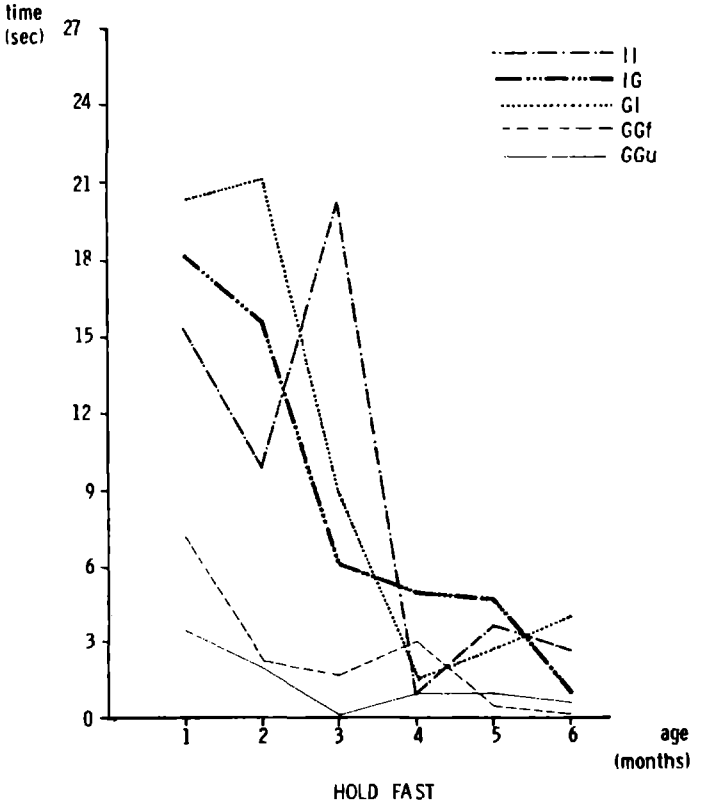
Rearing	1	137.25"	84.54"	Rearing cond.	1	75.81"	38.94"
Testpartner	1	36.02"	11.92"	Familiarity	1	31.93"	22.75"
Age	5	6.53"	4.49"	Age	5	3.88"	3.14"
Rearing X Partner	1	18.78"	2.86	Rearing X Age	5	17.69"	11.48"
Rearing X Age	5	18.37"	14.31"	Familiarity X Age	5	3.49"	2.33'
Partner X Age	5	2.53'	1.79	Error	162	26.72	137.64
Rearing X Partner X Age	5	3.71"	1.63				
Error	216	22.30	140.93				

' $.05 \geq p \geq .01$
" $.01 \geq p$

Table 13. F-values of frequencies and total time spent on the activities *investigate* and *anogenital inspection*.







Figs. 6, 7 and 8. Total time spent on the social contact activities *touch*, *take hold*, **and** *hold fast*.

TOUCH

	Df.	Freq.	Tot.time		Df.	Freq.	Tot.time
Rearing	1	9.11"	6.41'	Rearing cond.	1	15.27"	16.88"
Testpartner	1	0.12	0.21	Familiarity	1	0.01	0.03
Age	5	43.43"	37.53"	Age	5	35.11"	34.86"
Rearing X Partner	1	52.56"	44.03"	Rearing X Age	5	1.93	1.76
Rearing X Age	5	2.53'	2.52'	Familiarity X Age	5	0.55	0.42
Partner X Age	5	1.94	1.67	Error	162	45.11	46.93
Rearing X Partner X Age	5	12.76"	10.52"				
Error	216	56.34	67.41				

TAKE HOLD

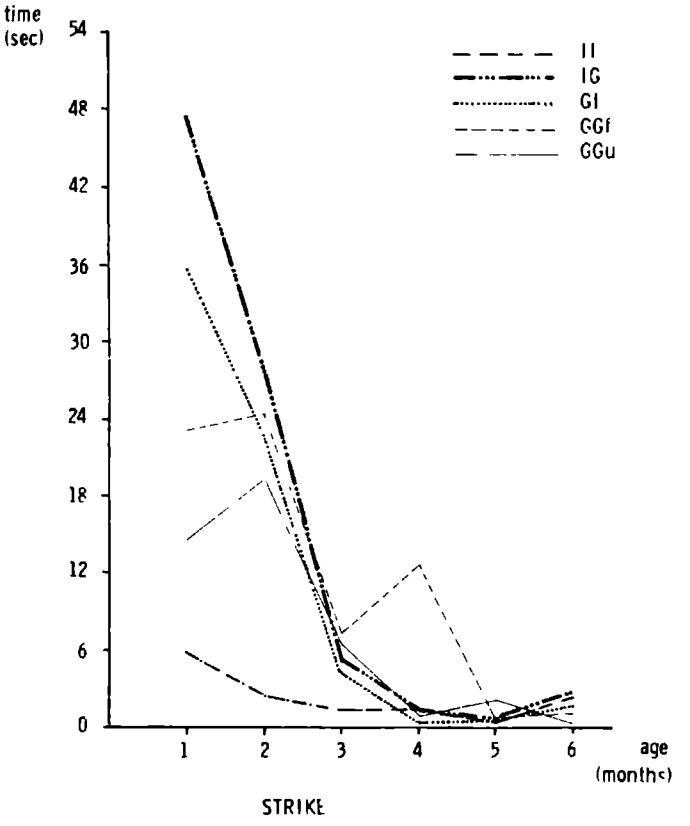
Rearing	1	0.99	0.87	Rearing cond.	1	11.27"	12.72"
Testpartner	1	0.01	0.02	Familiarity	1	0.01	0.02
Age	5	38.74"	34.52"	Age	5	35.47"	33.82"
Rearing X Partner	1	23.88"	25.39"	Rearing X Age	5	1.07	1.26
Rearing X Age	5	1.28	1.35	Familiarity X Age	5	0.49	0.43
Partner X Age	5	2.19	2.50'	Error	162	44.50	49.47
Rearing X Partner X Age	5	6.82	6.23"				
Error	216	51.82	58.87				

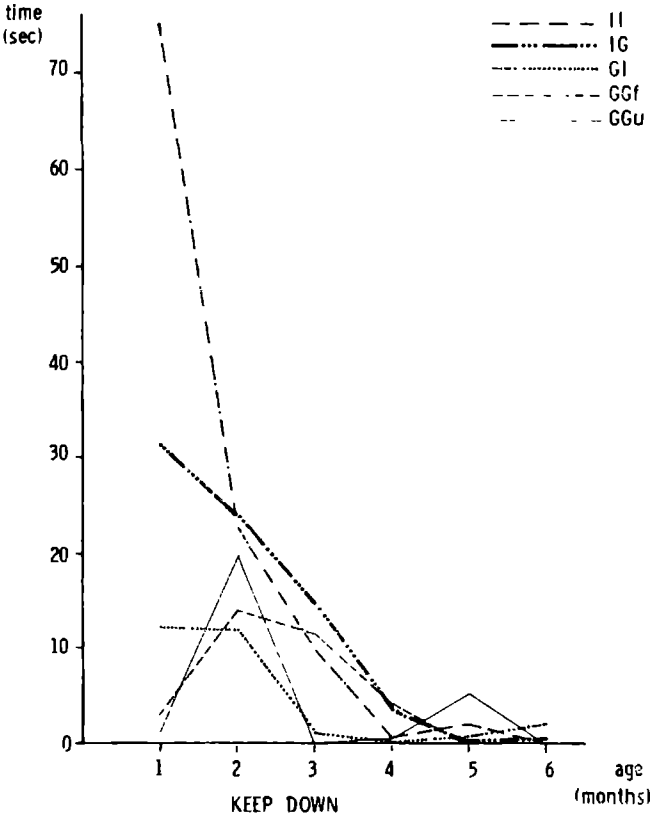
HOLD FAST

Rearing	1	1.06	2.90	Rearing cond.	1	46.48"	52.29"
Testpartner	1	11.80"	6.33'	Familiarity	1	2.20	1.03
Age	5	43.93"	6.44"	Age	5	27.76"	14.68"
Rearing X Partner	1	55.17"	5.22'	Rearing X Age	5	2.34'	2.94
Rearing X Age	5	0.30	0.57	Familiarity X Age	5	0.66	0.42
Partner X Age	5	1.82	1.29	Error	162	7.32	32.07
Rearing X Partner X Age	5	9.94"	1.89				
Error	216	9.04	184.83				

Table 14. F-values of frequencies and total time spent on activities *touch*, *take hold* and *hold fast*

' $.05 \geq p \geq .01$
" $.01 \geq p$





Figs. 9 and 10. Total time spent on the antagonistic offensive activities *strike* **and** *keep down*

STRIKE

	Df.	Freq.	Tot.time		Df.	Freq.	Tot.time
Rearing	1	0.08	0.59	Rearing cond.	1	26.40"	7.79"
Testpartner	1	18.51"	15.62"	Familiarity	1	2.57	4.51'
Age	5	87.08"	67.13"	Age	5	65.17"	41.80"
Rearing X Partner	1	75.89"	53.17"	Rearing X Age	5	0.94	2.45'
Rearing X Age	5	0.46	1.16	Familiarity X Age	5	1.23	1.10
Partner X Age	5	4.56"	3.99"	Error	162	26.83	119.19
Rearing X Partner X Age	5	31.44"	24.35"				
Error	216	18.28"	67.77				

KEEP DOWN

Rearing	1	15.23"	17.59"	Rearing cond.	1	21.27"	7.26"
Testpartner	1	0.93	1.60	Familiarity	1	0.17	0.09
Age	5	24.78"	14.65"	Age	5	25.66"	6.35"
Rearing X Partner	1	5.92"	1.30	Rearing X Age	5	3.93"	1.85
Rearing X Age	5	8.52"	8.26	Familiarity X Age	5	0.28	0.69
Partner X Age	5	1.29	3.55"	Error	162	10.76	301.89
Rearing X Partner X Age	5	1.43	1.26				
Error	216	9.46	400.41				

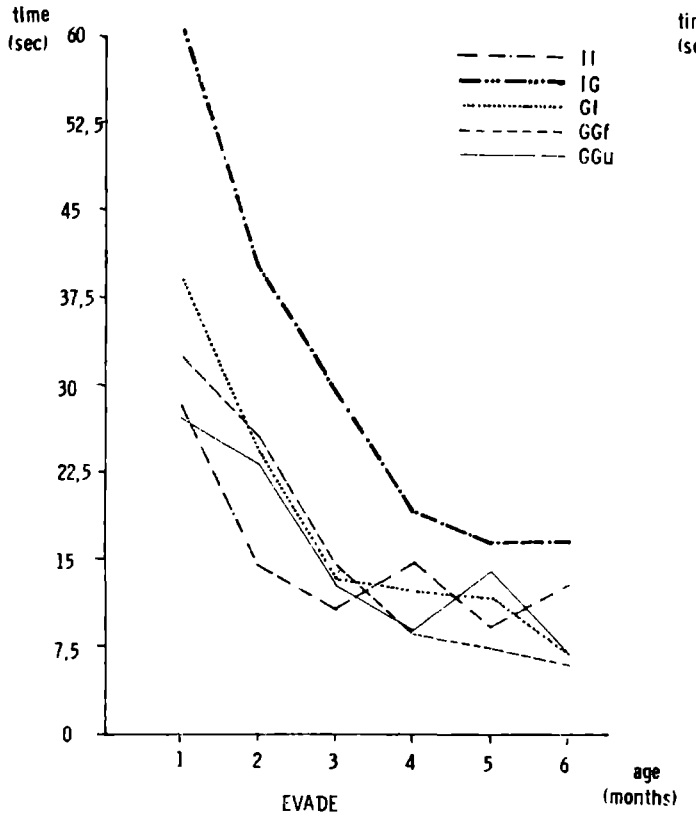
PUSH OVER AND BACKWARDS

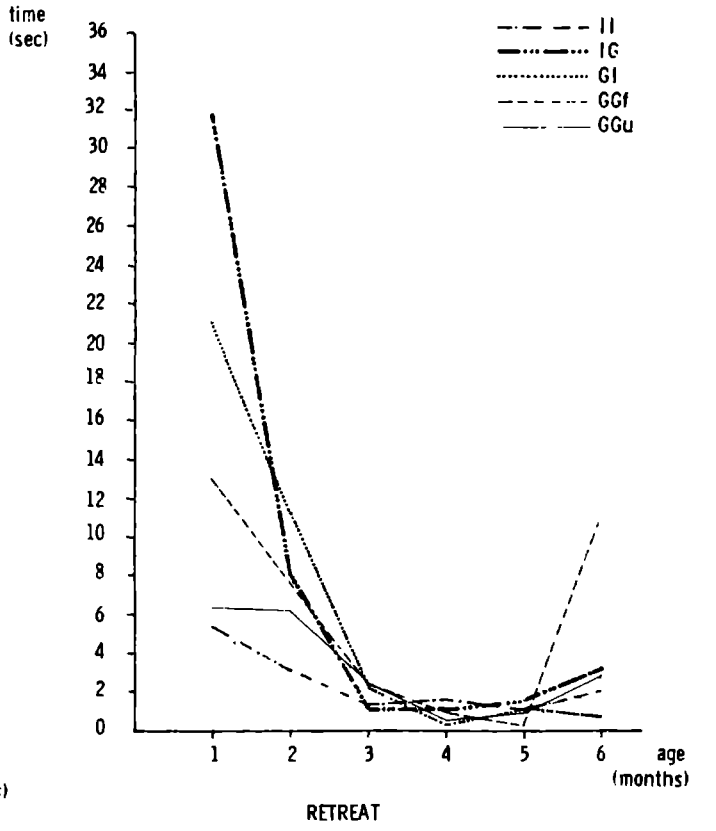
Rearing	1	18.02"	17.79"	Rearing cond.	1	55.83"	55.15"
Testpartner	1	1.16	0.40	Familiarity	1	0.66	0.69
Age	5	46.15"	45.31"	Age	5	32.71"	32.39"
Rearing X Partner	1	32.96"	29.41"	Rearing X Age	5	9.30"	9.15"
Rearing X Age	5	8.93"	7.96"	Familiarity X Age	5	0.30	0.30
Partner X Age	5	0.42	0.12	Error	162	14.51	14.74
Rearing X Partner X Age	5	9.44"	8.66"				
Error	216	13.77	14.87				

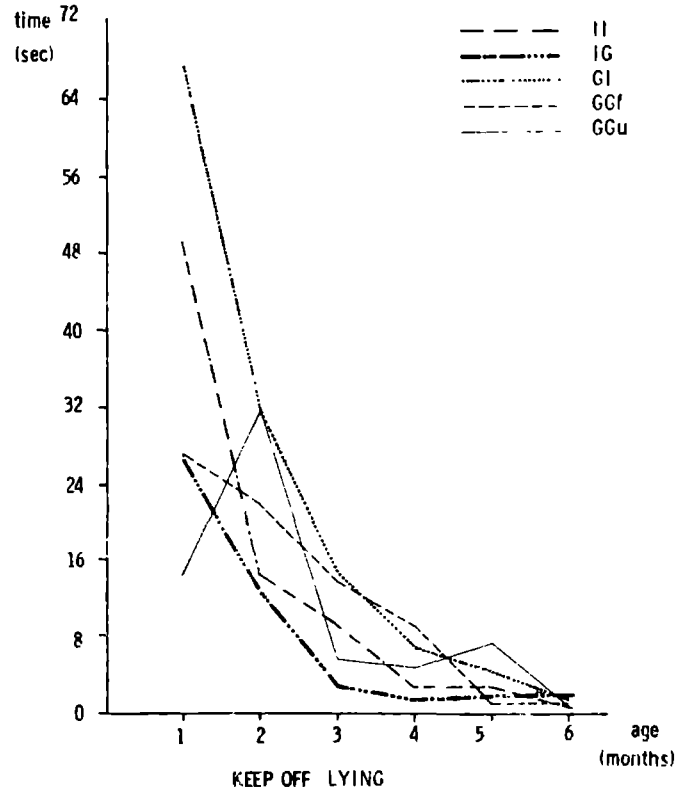
Table 15. F-values of frequencies and total time spent on activities *strike*, *keep down* and *push over and backwards*

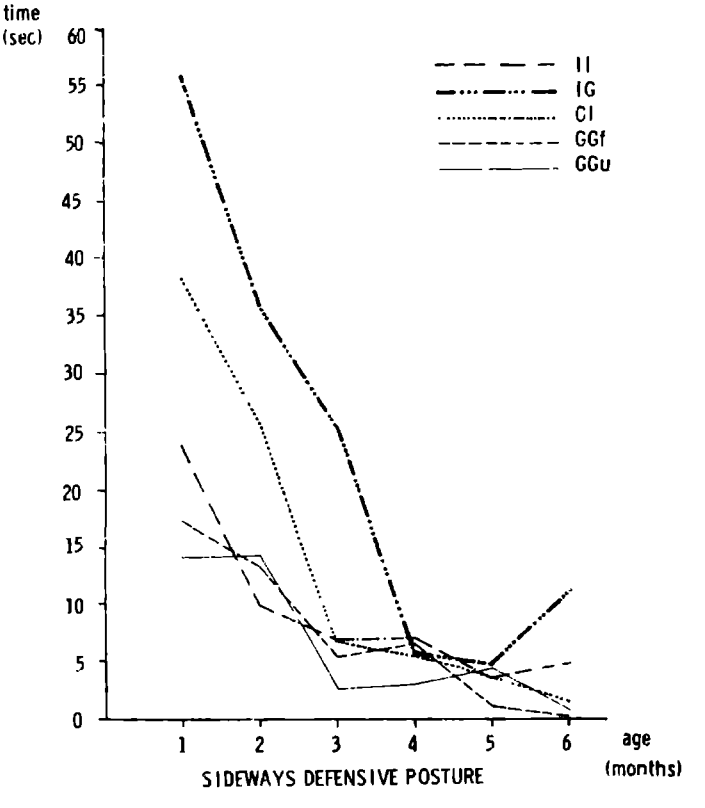
' .05 ⩾ p ⩾ .01

" .01 ⩾ p









Figs. 11, 12, 13 and 14. Total time spent on the antagonistic defensive activities *evade, retreat, keep off lying* **and the** *sideways defensive posture.*

EVADE

	Df.	Freq.	Tot.time		Df.	Freq.	Tot.time
Rearing	1	18.80"	19.66"	Rearing cond.	1	62.92"	63.68"
Testpartner	1	23.65"	23.22"	Familiarity	1	0.02	0.08
Age	5	39.99"	39.19"	Age	5	34.90"	33.45"
Rearing X Partner	1	43.17"	45.28"	Rearing X Age	5	0.52	0.58
Rearing X Age	5	1.22	1.35	Familiarity X Age	5	0.68	0.72
Partner X Age	5	2.15	1.97	Error	162	130.60	135.88
Rearing X Partner X Age	5	7.31"	6.61"				
Error	216	105.80	108.33				

RETREAT

Rearing	1	0.98	0.55	Rearing cond.	1	28.03"	4.30'
Testpartner	1	3.30	3.52	Familiarity	1	1.69	2.25
Age	5	67.32"	59.57"	Age	5	59.66"	15.72"
Rearing X Partner	1	53.20"	42.58"	Rearing X Age	5	4.33"	2.09
Rearing X Age	5	2.99'	2.90'	Familiarity X Age	5	1.33	0.75
Partner X Age	5	2.57'	2.35'	Error	162	22.83	97.16
Rearing X Partner X Age	5	30.57"	28.87"				
Error	216	18.20	23.88				

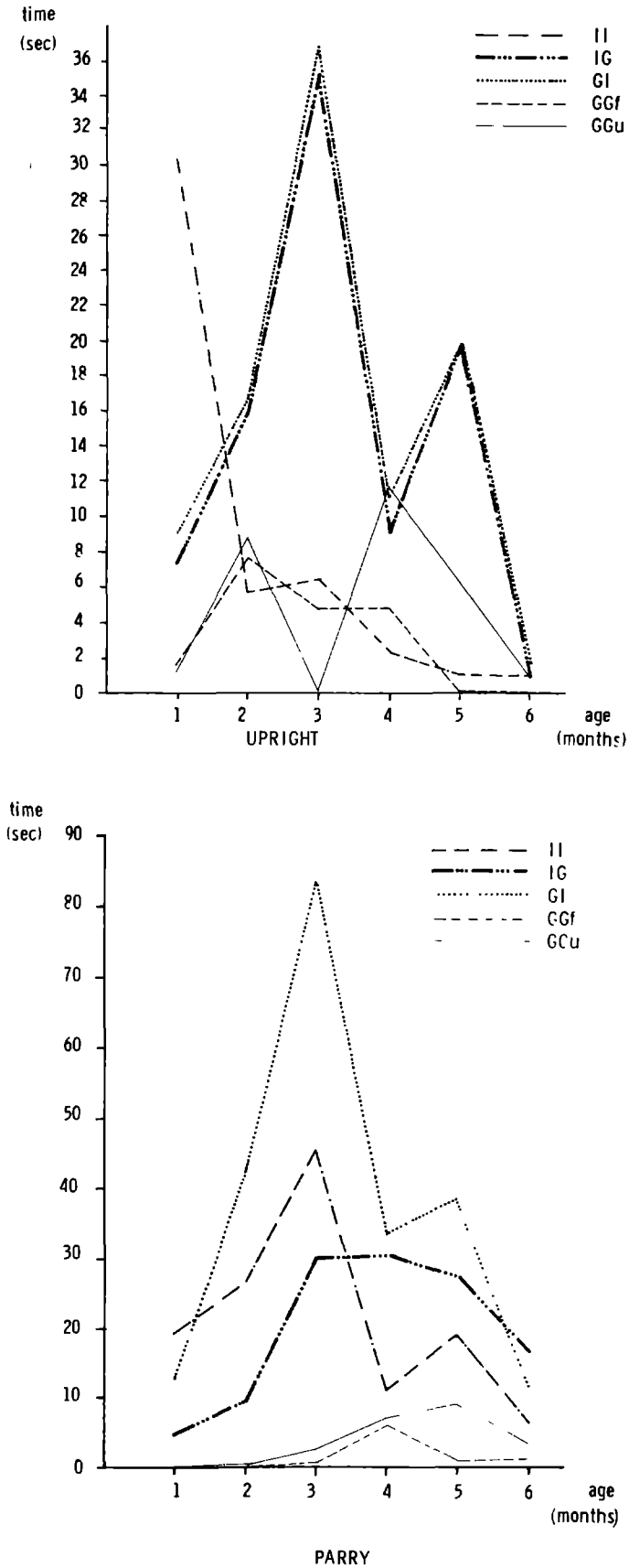
KEEP OFF LYING

Rearing	1	38.70"	7.89"	Rearing cond.	1	6.13'	2.37
Testpartner	1	8.93"	16.38"	Familiarity	1	1.40	0.33
Age	5	96.49"	40.30"	Age	5	40.98"	10.45"
Rearing X Partner	1	15.52"	1.67	Rearing X Age	5	4.99"	2.82'
Rearing X Age	5	4.73"	1.85	Familiarity X Age	5	2.86'	1.53
Partner X Age	5	9.02"	10.16"	Error	162	24.35	230.59
Rearing X Partner X Age	5	13.63"	1.78				
Error	216	22.58	219.58				

SIDEWAYS DEFENSIVE POSTURE

Rearing	1	5.85'	13.83"	Rearing cond.	1	45.62"	62.18"
Testpartner	1	3.19	4.15'	Familiarity	1	0.02	0.09
Age	5	43.87"	33.56"	Age	5	35.95"	26.51"
Rearing X Partner	1	34.25"	39.31"	Rearing X Age	5	1.21	2.19
Rearing X Age	5	1.47	1.73	Familiarity X Age	5	0.36	0.22
Partner X Age	5	0.93	0.82	Error	162	68.41	168.12
Rearing X Partner X Age	5	8.30"	7.60"				
Error	216	70.27	164.05				

Table 16. F-values of frequencies and total time spent on activities *evade*, *retreat*, *keep off lying* and *sideways defensive posture*
' .05 ⩾ p ⩾ .01; " .01 ⩾ p



Figs. 15 and 16. **Total time spent on the antagonistic ambivalent activities** *upright* **and** *parry*

UPRIGHT

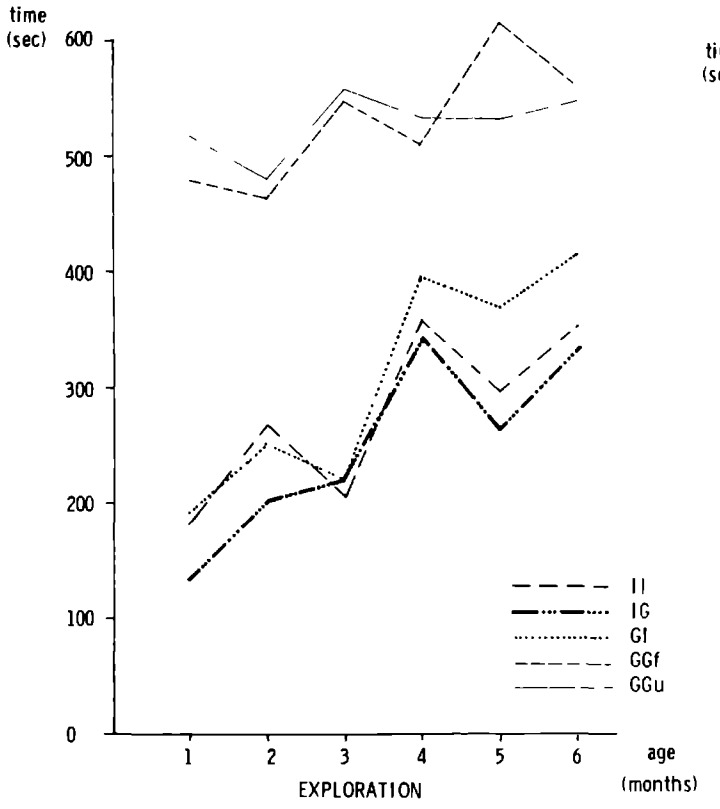
	Df.	Freq.	Tot.time		Df.	Freq.	Tot.time
Rearing	1	0.00	0.14	Rearing cond.	1	24.69"	19.65"
Testpartner	1	0.52	0.71	Familiarity	1	0.09	0.38
Age	5	10.69"	4.04"	Age	5	7.33"	4.63"
Rearing X Partner	1	40.77"	13.09"	Rearing X Age	5	2.02	2.52'
Rearing X Age	5	0.64	1.30	Familiarity X Age	5	0.60	0.38
Partner X Age	5	1.13	1.39	Error	162	15.65	231.91
Rearing X Partner X Age	5	5.85"	5.50"				
Error	216	15.54	361.71				

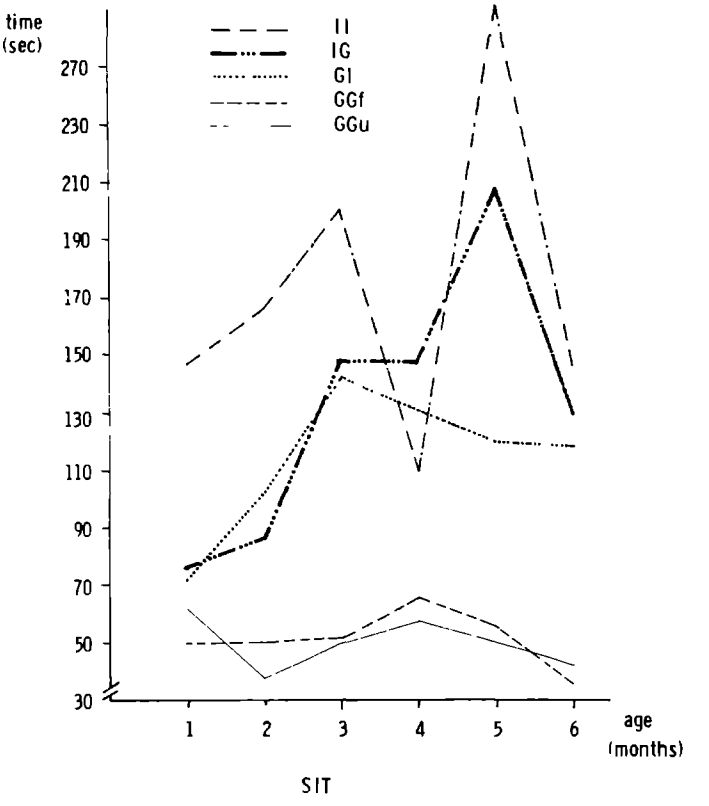
PARRY

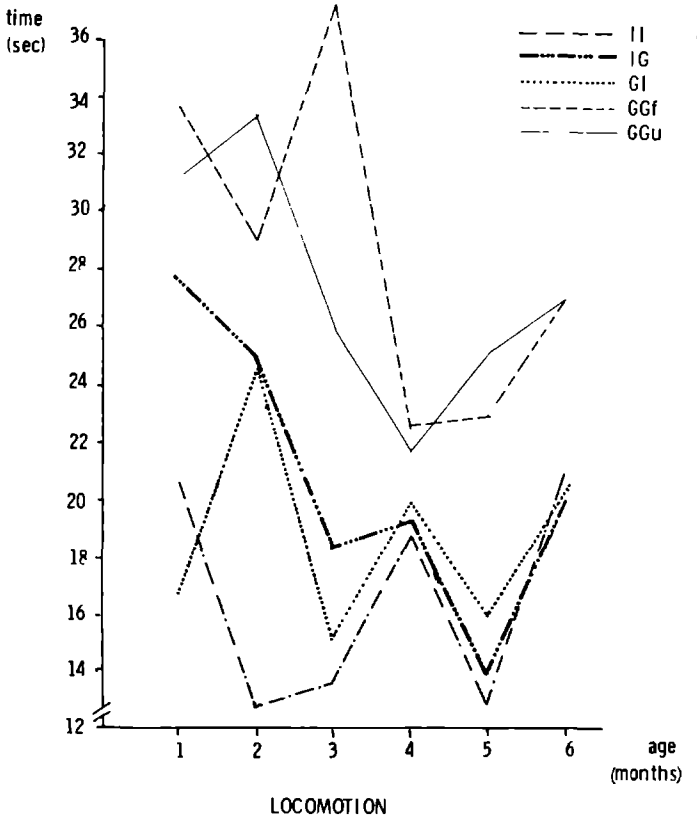
Rearing	1	0.21	0.01	Rearing cond.	1	65.26"	43.08"
Testpartner	1	24.13"	18.80"	Familiarity	1	0.93	0.63
Age	5	5.83"	5.41"	Age	5	5.09"	4.34"
Rearing X Partner	1	23.96"	15.59"	Rearing X Age	5	0.78	0.70
Rearing X Age	5	0.36	0.17	Familiarity X Age	5	0.64	0.17
Partner X Age	5	2.78'	3.50"	Error	162	19.86	278.69
Rearing X Partner X Age	5	1.90	1.40				
Error	216	58.70	956.93				

' $.05 \geqslant p \geqslant .01$
" $.01 \geqslant p$

Table 17. F-values of frequencies and total time spent on activities *upright* and *parry*







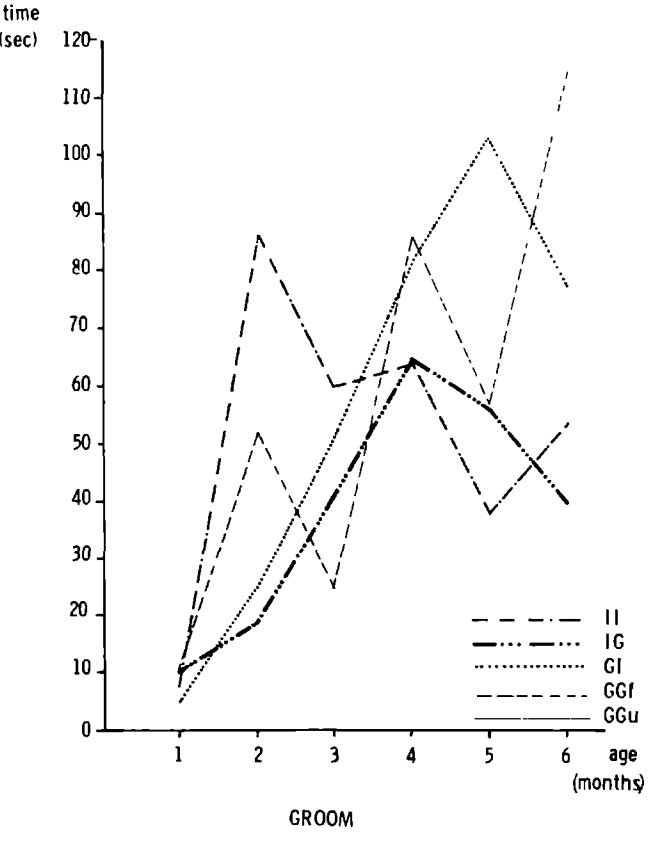


Fig. 17, 18, 19 and 20. Total time spent on the non-social activities *exploration, sit, locomotion* **and** *groom.*

EXPLORATION

	Df.	Freq.	Tot.time		Df.	Freq.	Tot.time
Rearing	1	57.75"	139.50"	Rearing cond.	1	83.07"	306.33"
Testpartner	1	38.08"	55.23"	Familiarity	1	0.94	0.00
Age	5	5.87"	15.71"	Age	5	3.92	7.03"
Rearing X Partner	1	6.38'	89.47"	Rearing X Age	5	4.43"	2.10
Rearing X Age	5	2.00	0.96	Familiarity X Age	5	0.43	0.97
Partner X Age	5	1.13	2.49'	Error	162	316.59	10085.48
Rearing X Partner X Age	5	1.54	2.14				
Error	216	433.44	10253.51				

SIT

Rearing	1	47.23"	68.38"	Rearing cond.	1	113.14"	159.82"
Testpartner	1	13.65"	37.24"	Familiarity	1	0.23	0.09
Age	5	5.55"	6.44"	Age	5	3.73"	9.93"
Rearing X Partner	1	22.46"	1.81	Rearing X Age	5	5.25"	4.36"
Rearing X Age	5	2.90'	4.17"	Familiarity X Age	5	0.36	0.17
Partner X Age	5	0.85	1.07	Error	162	99.79	1689.70
Rearing X Partner X Age	5	4.24"	1.93				
Error	216	140.71	4501.19				

LOCOMOTION

Rearing	1	23.19"	13.76"	Rearing cond.	1	33.14"	22.59"
Testpartner	1	38.56"	27.50"	Familiarity	1	1.52	0.44
Age	5	3.03'	4.11"	Age	5	4.71"	5.16"
Rearing X Partner	1	2.38	3.20	Rearing X Age	5	1.40	1.44
Rearing X Age	5	1.39	1.65	Familiarity X Age	5	1.38	1.44
Partner X Age	5	2.38'	1.84	Error	162	58.16	92.23
Rearing X Partner X Age	5	1.06	0.61				
Error	216	54.94	87.29				

GROOM

Rearing	1	0.18	2.93	Rearing cond.	1	0.02	5.35'
Testpartner	1	0.00	4.69'	Familiarity	1	0.07	1.26
Age	5	7.48"	13.51"	Age	5	2.88'	8.60"
Rearing X Partner	1	0.12	0.27	Rearing X Age	5	0.39	4.55"
Rearing X Age	5	0.51	3.59"	Familiarity X Age	5	0.63	1.65
Partner X Age	5	1.50	1.47	Error	162	13.65	1738.65
Rearing X Partner X Age	5	0.64	3.31"				
Error	216	14.65	1458.61				

Table 18. F-values of frequencies and total time spent on activities *exploration*, *sit*, *locomotion* and *groom*

' $.05 \geq p \geq .01$

" $.01 \geq p$

FALL SIDEWAYS OR BACKWARDS	Rearing	1	0.04	0.17
	Testpartner	1	13.21"	11.70"
	Age	5	53.06"	42.22"
	Rearing X Partner	1	36.99"	22.56
	Rearing X Age	5	0.62	0.68
	Partner X Age	5	6.11"	4.75"
	Rearing X Partner X Age	5	10.36"	6.45"
	Error	216	11.75	16.62
STRETCHED ATTENTION	Rearing	1	0.10	0.00
	Testpartner	1	4.82'	2.68
	Age	5	13.68"	5.02"
	Rearing X Partner	1	2.87	2.01
	Rearing X Age	5	0.71	1.91
	Partner X Age	5	1.01	0.90
	Rearing X Partner X Age	5	2.80'	0.33
	Error	216	4.23	66.54
ORAL INSPECTION	Rearing cond.	1	24.46"	15.64"
	Familiarity	1	22.65"	23.44"
	Age	5	1.28	2.15
	Rearing X Age	5	0.82	1.03
	Familiarity X Age	5	2.99'	3.46"
	Error	162	1.80	3.99
NOSING	Rearing cond.	1	26.41"	15.99"
	Familiarity	1	4.39'	2.27
	Age	5	3.97"	4.70"
	Rearing X Age	5	7.39"	7.46"
	Familairity X Age	5	3.25"	2.13
	Error	162	1.09	1.47

Table 19. F-values of frequencies and total time spent on the activities *fall sideways or backwards*, *stretched attention*, *oral inspection* and *nosing*.

' $.05 \geqslant p \geqslant .01$

" $.01 \geqslant p$

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CURRICULUM VITAE

Ger Peijs werd geboren op 15 augustus 1945 te Tegelen. Na de lagere school te hebben doorlopen, bezocht hij het St. Thomascollege te Venlo. Daar behaalde hij in 1964 het diploma Gymnasium β. In dat jaar schreef hij in voor de studie psychologie aan de Katholieke Universiteit te Nijmegen. Het doktoraalexamen psychologie, hoofdvak Vergelijkende en Fysiologische Psychologie, legde hij af in 1972. Per september 1972 maakte hij als wetenschappelijk medewerker deel uit van de Nederlandse werkgroep voor research van "Agressief gedrag" . Zijn bijdrage bestond uit het doen van ethologisch onderzoek naar ontwikkelingsaspekten van agressief gedrag. De onderzoeken voerde hij uit op de afdeling Vergelijkende en Fysiologische Psychologie van de Katholieke Universiteit te Nijmegen.

Op 1 april 1976 trad hij in een gekombineerde funktie in dienst van de Stichting St. Jozefsheil en Jan de Witkliniek te Bakel (N.Br.) en het R.K. Kempisch Verpleeghuis te Bladel (N.Br.). Per 1 mei 1977 aanvaardde hij een volledig dienstverband als klinisch psycholoog aan het Verpleegcentrum Bakel.

STELLINGEN.

1. Bij het doen van ethologisch onderzoek naar de ontogenie van gedrag is het onontbeerlijk het volwassen repertoire van de te bestuderen soort te kennen.

2. Sociale isolatie van de rat gedurende een daarvoor gevoelige periode in de ontwikkeling leidt tot verstoring van de balans tussen naderingsgedrag en ontwijkingsgedrag.

3. Sociale isolatie van een zich ontwikkelend sociaal organisme is een ingreep die wezenlijk verschillend is van sociale isolatie van dat organisme op volwassen leeftijd.

4. Het is zeer aanvechtbaar dominantie, gemeten in zgn. "dominance tube" proefopstellingen te interpreteren als uiting van een hoge agressieve motivatie in de rat.

5. De huisvesting van dieren in laboratoria is veelal onvoldoende afgestemd op het soort onderzoekingen waarin de dieren gebruikt (gaan) worden.

6. Er van uit gaande dat de uitspraak "mens sana in corpore sano" waarheidskarakter bezit, moet men vrezen dat het, gelet op de hedendaagse ontwikkelingen in de topsport, ook met de lichamelijke gezondheid van topsportbeoefenaren, niet best gesteld is.

7. Uit een oogpunt van sociaal-hygiënische overwegingen dient te worden vastgesteld dat de aanwezigheid van de psycholoog in het verpleeghuis van meer wezenlijk belang is voor het welbevinden van de verpleeghuisbewoner dan de aanwezigheid van deze bewoner zelf.

8. Het verpleeghuis dient, gelet op zijn doelstellingen en ook al om louter financiële redenen, te overwegen de richtlijnen van het Centraal Orgaan Ziekenhuistarieven met betrekking tot de getalsverhouding gediplomeerden - leerling ziekenverzorgenden, aan verpleeghuizen verbonden, naast zich neer te leggen. Deze richtlijnen worden als alibi gehanteerd voor het gebruik van "disposable" ziekenverzorgenden.

9. Een grondig psychodiagnostisch onderzoek zowel van de demente mens alsook, indien mogelijk, van het verplegend en verzorgend personeel is onontbeerlijk voor het scheppen van een goed, individueel gericht, therapeutisch klimaat rondom die mens.

10. Het getuigt van onterechte hovaardigheid en geringe kennis van zaken kwalifikaties als"beestachtig" en "dierlijk" te gebruiken ter beschrijving van zogenaamd onmenselijk, niet-menselijk gedrag.

11. Spreiding van kennis kent zijn grenzen, zodra het om spreiding van kennis omtrent personen gaat.

12. Het feit dat de promovendus na het schrijven van zijn dissertatie de overtuiging is toegedaan dat het proefschrift er heel anders uit zou zien mocht hij nogmaals voor dezelfde taak gesteld worden, dient gezien te worden als symptomatisch voor de ambivalente gevoelens die inherent zijn aan de voltooiing van het werkstuk.

Nijmegen, 22 juni 1977. G.L.A.M. Peijs.